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Effects of Phosphorus Loading on Phytoplankton Distribution and Certain Aspects of Cytology in Saginaw Bay, Lake Huron

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Saginaw Bay has always been one of the more productive regions of the Great Lakes system. At the present time, it is also one of the most modified. Excessive nutrient and conservative element loadings are factors which have led to severe perturbation of primary producer communities in the region. Because of the physical dynamics of the bay region, idealized dilution gradients are grossly modified by transport of water masses and their entrained chemical constituents, fauna and flora into, as well as away from, the bay. However, there appears to be considerable selection among population components of the assemblages transported. For example, blue-green algae appear to be conserved in the bay while diatoms are subjected to great losses.

The major effort in this investigation was to provide data on phytoplankton biovolume which would support a model of processes occurring in Saginaw Bay. A method of estimating the actual viable fraction of the cell volumes of representatives of the various physiological groups of phytoplankton found in Saginaw Bay was developed, and polyphosphate body formation was studied. Results showed that substantial phytoplankton populations were exported from the bay to Lake Huron. Under average wind conditions, most export occurred along the southern coast. These populations were then entrained in the general Lake Huron circulation and were spread down the Michigan coast southward from the bay. Under certain advective conditions, however, phytoplankton were discharged from the bay either to the north or directly offshore.

Cytological analysis showed that many species sequestered phosphorus in excess of their immediate physiological needs, in the form of polyphosphate bodies. Populations exported from the bay also contained these polyphosphate bodies. Analysis of the polyphosphate bodies showed that significant quantities of certain toxic metals, notably lead, were incorporated into these inclusions.

Analysis of the relationship of total phytoplankton cell volume to protoplasmic constituent volume showed that crude cell volume measurements furnished a poor estimate of actual living biomass in many populations. It was concluded that more refined techniques are required to correctly convert estimates of cell number to estimates of biomass.

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EFFECTS OF PHOSPHORUS LOADING ON PHYTOPLANKTON DISTRIBUTION AND CERTAIN ASPECTS OF CYTOLOGY IN SAGINAW BAY, LAKE HURON

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ABSTRACT

Phytoplankton abundance and species composition in Saginaw Bay reflects very high nutrient and conservative ion loadings. Typical of nutrient stressed systems, seasonal succession and areal distribution are highly variable, and large abundance and composition changes may be generated by local meteorological events. Spring flora are dominated by diatoms such as *Fragilaria capucina* and *Stephanodiscus binderanus*, which are associated with the most eutrophied regions in the Great Lakes. Atypically large numbers of benthic diatoms occur in Saginaw Bay plankton. Following the spring diatom bloom, assemblages become dominated by blue-green and green algae, apparently due to rapid silica depletion. Nuisance populations such as *Aphanizomenon flos-aquae* and *Anacystis cyanea* are common. In late summer there is a second increase in diatom abundance, apparently due to regeneration and recirculation of silica from the sediments. This secondary diatom bloom is composed of species such as *Actinocyclus normanii* var. *subsalsa* and *Melosira granulata*.

Our results show substantial export of phytoplankton populations from the bay to Lake Huron. Under average wind conditions, most export occurs along the southern coast and these populations are then entrained in the general Lake Huron circulation and spread down the Michigan coast southward from the bay. Under certain advective conditions, however, phytoplankton may be discharged from the bay either northward or directly offshore.

Cytological analysis shows that many of the species present sequester phosphorus in excess of their immediate physiological needs in the form of polyphosphate bodies. Polyphosphate body formation may be triggered by conditions which interfere with normal phosphorus metabolism. These include phosphorus starvation followed by excess resupply, deficiencies in other essential nutrients, or toxic effects which limit growth but not phosphorus uptake. All of these conditions may occur in Saginaw Bay. Our analysis further shows that populations exported from the bay contain excess phosphorus and this biologically entrained loading may affect other areas of southern Lake Huron.

Analysis of polyphosphate bodies also shows that significant quantities of certain toxic trace metals, notably Pb, are incorporated into these inclusions. The ultimate fate of this material has not been demonstrated, but it may represent a previously unrecognized type of biological incorporation and transport important in some areas of the Great Lakes.

We also investigated the relationship of total phytoplankton cell volume to protoplasmic constituent volume using quantitative morphometric techniques. This analysis shows that crude cell volume furnishes a poor estimate of actual living biomass in many populations, and indicates that more refined techniques are necessary to correctly convert estimates of cell number to estimates of biomass.

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INTRODUCTION

Saginaw Bay has probably always been one of the more productive regions within the Great Lakes system. The productivity of the fishery resource was undoubtedly one of the factors attracting early settlement in the area. Other natural resources of the drainage basin provided the incentive for early settlement and substantial economic growth in the region. The timber resources of the Saginaw River and its tributaries were rich and easily accessible which led to early development of the area and the establishment of an early industrial base. Once cleared of its natural vegetation, much of the land was found suitable for intensive agricultural practices. Finally, the presence of subsurface resources, primarily petroleum and salt, made possible the establishment of one of the midwest's centers of chemical industry. Unfortunately, the development of the Saginaw-Bay City-Midland industrial complex and intensive regional agriculture proceeded at the expense of severe deterioration of water quality within Saginaw Bay. At the present time it is one of the most seriously modified parts of the Great Lakes system. During the past few decades Saginaw Bay has been beset with water quality problems including obnoxious algal blooms, taste and odor problems in municipal water supplies, and fish flesh tainting. The history of these problems and the context of the present investigation have been outlined by the International Joint Commission (1976). The literature pertaining to pollution problems in Saginaw Bay has been reviewed by Freedman (1974) and need not be extensively recapitulated here. It should be pointed out, however, that the perturbation of primary producer communities in this region reflects the effects of many factors. The most obvious of these are the effects of excessive nutrient loadings. At the present time the waters of Saginaw Bay are probably the most productive in the entire Great Lakes system. The composition of the phytoplankton and benthic algal flora also reflects the effects of extreme conservative element loadings. Although these loadings have apparently been decreased to some degree in recent years (Smith et al., 1977), the flora of the bay still contains many elements usually found in brackish water localities. Finally, although not experimentally documented, certain population distributions within the bay can most plausibly be explained by direct toxic effects.

Saginaw Bay is also an extremely dynamic system. There are strong gradients in almost all factors of physiological interest between the lower bay and the open waters of Lake Huron. As might be expected, these gradients are reflected in the population and community responses of the phytoplankton flora. This situation is complicated by the physical dynamics of the system (Richardson, 1974). Idealized dilution gradients are grossly modified by mass transport of water masses and their entrained chemical constituents, fauna, and flora into and away from the bay. Schelske et al. (1974) have demonstrated the transport of populations developed in Saginaw Bay into the open waters of Lake Huron. One of the most interesting aspects of this study is the fact that there appears to be considerable selection among the population components of the assemblage being transported. Certain populations, primarily blue-green algae, appear to be conserved, in the sense that their abundance is highly correlated with the concentration of biologically conservative chemical elements being discharged from the bay. Other populations, primarily diatoms, are apparently subjected to much greater losses during transport. Because of the different physical characteristics of the populations involved, it is attractive to attribute such losses to sinking. Without further direct evidence, however, other possible losses, such as predation or direct cell death and lysis, cannot be excluded. Equally interesting, conservation of mass demands that transient mass flow export of water from Saginaw Bay be compensated by import of water masses from Lake Huron. Such water masses contain biological communities adapted to physical and chemical conditions found in the open lake. As they are diluted with, and enriched by, Saginaw Bay water such populations might be expected to undergo variable responses ranging from death to growth stimulation depending on both their own physiological requirements and the degree and rate of mixing.

A meaningful analysis of such a dynamic system requires either extremely intensive sampling, both areally and timewise, or recourse to simulation of the system from a more limited measurement base. Since a sampling program of the density demanded is probably beyond the available regional resources, and the simulation approach offers the additional advantage of making more reasonable forecast and hindcast projections, the primary emphasis in this project was directed toward facilitating this type of analysis. A number of types of information regarding phytoplankton are necessary. Since any assemblage is likely to contain representatives of several major physiological groups with differing absolute or relative nutrient requirements, it is necessary that qualitative information be retained in the model data input. It is also necessary that the input be in some uniform measure. Since phytoplankton cells vary considerably in size, even within a given species, it is highly attractive to rely upon some secondary estimate of biomass such as total carbon or extracted chlorophyll.

Unfortunately this approach, although the one generally utilized in such studies, is subject to a number of difficulties and the correlation between such measures and independent estimates of phytoplankton biomass for assemblages occurring in the Great Lakes is often surprisingly low (Vollenweider et al., 1974). Although considerably more laborious, direct enumeration of the cells present and subsequent reduction of this information to some standard unit appears to offer a desirable alternative, especially since qualitative information can be preserved in the resultant data set. Although perhaps the most desirable approach, this method is not without its own significant difficulties. The most generally utilized approach is to estimate the volume of the cells present, then to directly convert the volumetric estimate to mass. As may be easily appreciated, precise estimates of volume are difficult to obtain because of the complex form of many species and the degree of variability present in many populations. A fundamentally more serious problem is the variation in cytologic structure and composition between the major physiological groups of phytoplankton or, in some cases, within members of a single division. It has long been recognized (Lohmann, 1908) that relatively large proportions of the total volume of the cells of certain phytoplankton species are constituted by their vacuoles. If the fractional volume constituted by metabolically inert wall materials is added to this, it is easy to see that direct conversions from cell volume to estimates of biomass are difficult to interpret precisely. It is indeed unfortunate that estimates of phytoplankton abundance in the current literature are reported in units of "biovolume" since this neither provides an unambiguous estimate of biomass nor preserves individual population abundance information. Perhaps the most commonly utilized method of converting phytoplankton abundance estimates to estimates of biomass is regression of cell volume or plasma volume estimates on independent estimates of cell carbon content (Strathmann, 1967). While this method may be applicable when dealing with relatively homogeneous oceanic phytoplankton assemblages, it is somewhat questionable in a situation such as Saginaw Bay which has exceedingly diverse assemblages containing many pseudoplanktonic or tychoplanktonic populations.

These considerations make it evident that determination of precise estimates of phytoplankton composition and biomass within the Saginaw Bay system is a considerable challenge within the inevitable constraints of available resources. Additional constraints are introduced by consideration of the overall project objectives. The entire investigation involved the first really large scale investigation on the Lake Huron system and consisted of several components. Although each of the components was the prime responsibility of a separate laboratory, they are linked to the project reported here through a common sampling base. In some cases the data generated by this project have been incorporated into the results of other projects. The major projects interfacing with this one are the following:

1. A study of physical and chemical conditions in Saginaw Bay reported by Smith et al. (1977).

2. Construction of a process oriented model of Saginaw Bay reported by Biermann et al. (1980). One of the major efforts in the present investigation was the generation of phytoplankton volume/abundance estimates which provided a major input to the above study. The synthesized results of this effort are reported there.

3. Studies of the distribution of primary consumer organisms in Saginaw Bay and southern Lake Huron (Gannon, in prep., Stemberger et al. (1979).

4. Studies of physical and chemical conditions and biological productivity in southern Lake Huron by Schelske et al. (1980).

5. A study of phytoplankton abundance and distribution in southern Lake Huron by Stoermer and Kreis (1980).

MAJOR COMPONENTS OF THIS PROJECT

The major effort in this investigation was to provide data on phytoplankton biovolume to support a model of processes in Saginaw Bay. This information has been reported by Beirmann et al. (1980). For purposes of the model, the data were summarized in categories representing the major physiological groups of phytoplankton which occupy the base. It was felt that the actual numbers of organisms and the time sequence of development are also important in interpreting trends within the bay. This information is reported in the first section of the present report.

The interpretation of cell volumes in terms of biomass, although demonstrably preferable to traditional methods of biomass estimation, contains certain problems which have not been adequately addressed. As part of this study, we undertook research directed to developing a method of estimating the actual viable fraction of the cell volumes of representatives of the various physiological groups of phytoplankton found in Saginaw Bay. The results of this study are presented in Section 2 of this report.

Relatively early in the project it became apparent that at least certain populations generated within Saginaw Bay exhibit delayed response to phosphorus enrichment, or at least thrive far beyond the zones of the bay most directly affected by high phosphorus loadings. Since some blue-green algal populations contained polyphosphate bodies apparent at the light microscope level, we undertook further research to investigate several questions:

1. Are polyphosphate bodies quantitatively important in some of the more abundant potential nuisance organisms, particularly species of blue-green algae?

2. Are the bodies present in populations advected from the bay in sufficient quantitatives to allow further growth of potential nuisance organisms in southern Lake Huron?

3. Are the eukaryotic organisms which display distribution patterns similar to thse blue-green algal populations also capable of storing excess phosphorus in areas of high loading and subsequently metabolizing it after being advected into areas not receiving direct loadings?

The results of this study are reported in Section 3 of this report. Also, as part of this study, we discovered that appreciable quantities of certain heavy metals, particularly Pb, are also sequestered in polyphosphate bodies in Saginaw Bay phytoplankton. These observations have been separately published (Stoermer et al., 1980).

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SECTION 1

DISTRIBUTION OF MAJOR PHYTOPLANKTON GROUPS

MATERIALS AND METHODS

The samples utilized in this study were taken in conjunction with water chemistry and zooplankton samples as part of the combined study discussed above. The general sampling strategy employed has been discussed by Smith et al. (1977) and will not be recapitulated here.

In most instances phytoplankton samples were taken by submersible pump. In some cases either Niskin or Van Dorn bottles were used due to mechanical failures of the pumping system. In all cases the phytoplankton samples were taken in 125 ml polyethylene bottles and fixed with 4% (vol./vol.) glutaraldehyde immediately upon collection. Samples were kept on ice in darkness until they were processed into slides.

Material was prepared for analysis by the membrane clearing technique (Schelske et al., 1976). In most instances 50 ml of the original fixed sample was prepared. Due to the extremely dense phytoplankton assemblages encountered at some stations, it was necessary to reduce the volume filtered in some preparations to either 25 or 12.5 ml.

Population estimates were developed from replicate 1 mm strip counts of randomly selected areas of the slide preparations. Populations present were enumerated and the mean dimensions of the taxa were recorded. Estimates of the volume of the phytoplankton present were developed from calculations based on approximate shape formulae of the species present. The volume data were converted to an estimate of carbon biomass (Bierman et al., 1980).

Material fixed according to the schedule used for preparation for electron microscopy (see Section 2) was used for verification of identifications in some instances, since this procedure finishes superior preservation of cellular structure.

The first sampling cruise took place 25 March. Relatively few stations were actually sampled due to adverse weather conditions. Diatoms were dominant in the samples taken, with very large populations present at one station in the southeastern sector (Fig. 1). The abundance of diatoms at this station dominated the total abundance pattern, since other stations had much smaller phytoplankton densities. Other groups were of minor importance. Green and blue-green algae were noted at scattered stations, but heterocyst forming blue-greens were totally absent. Flagellates were present at all stations, but did not approach diatoms in total numbers.

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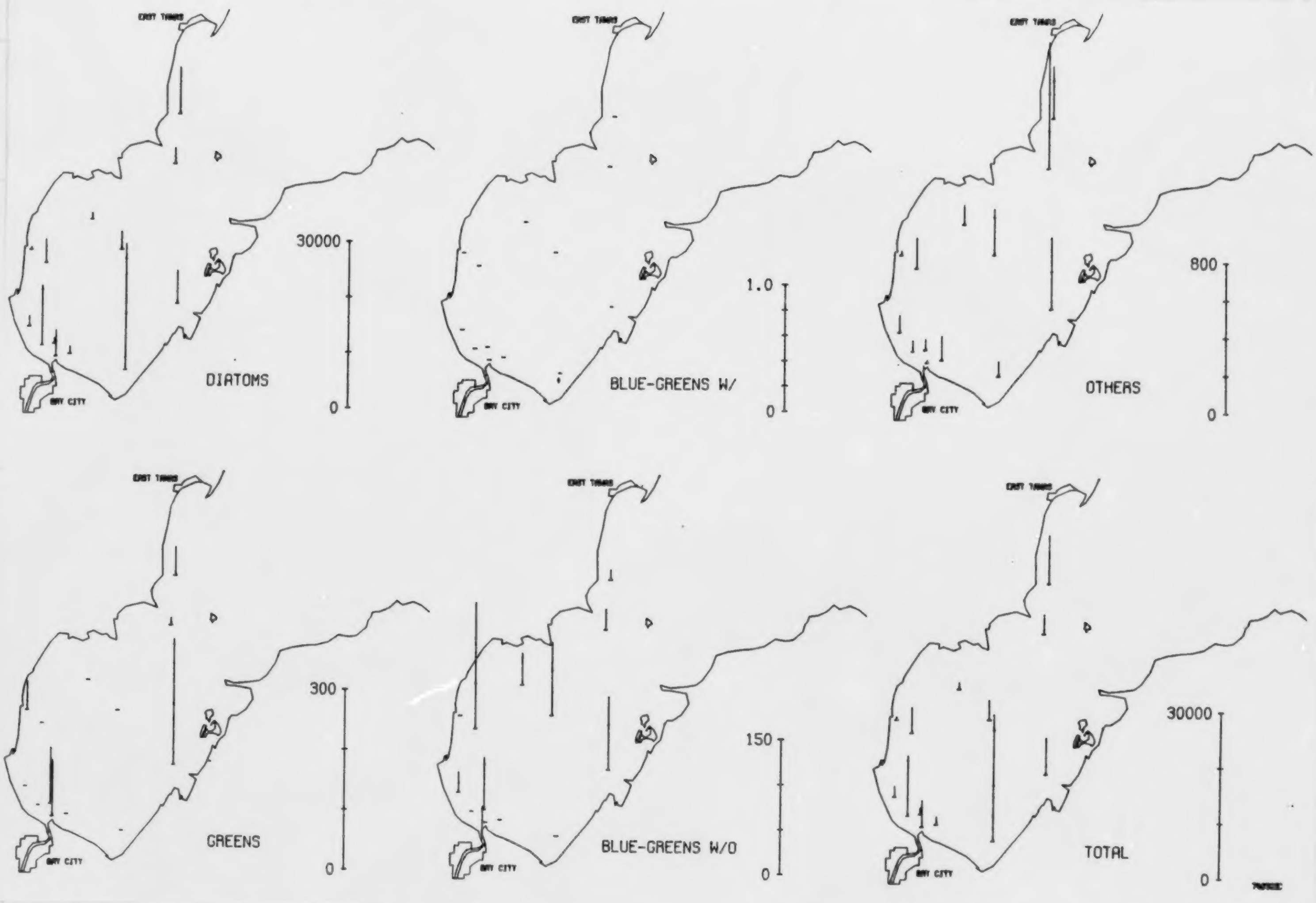
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Figure 1. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 25 March 1974.

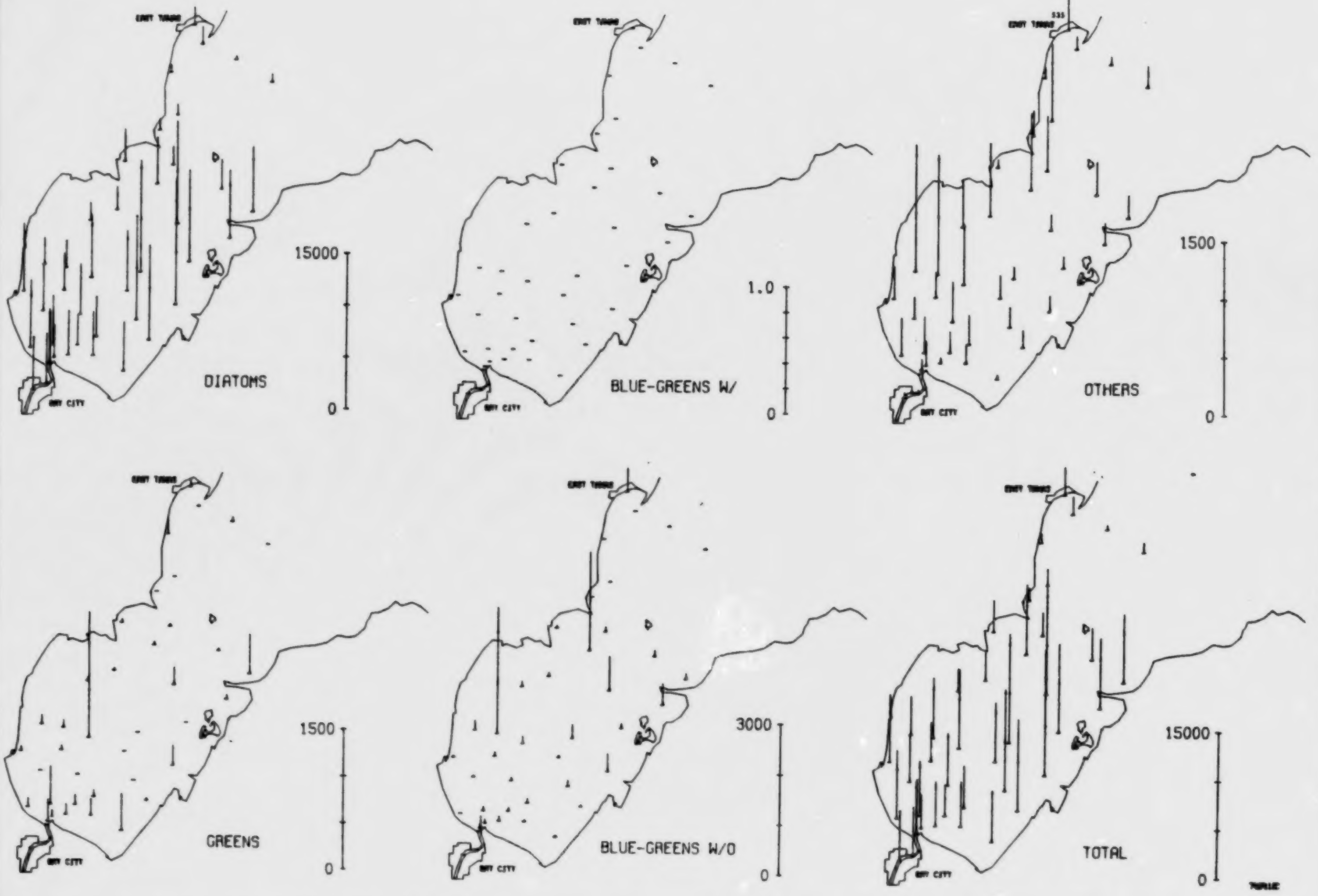
Much more complete sampling, particularly of the lower bay, was accomplished during the second cruise which began 16 April (Fig. 2). Although no station achieved the very high total phytoplankton density noted during the previous cruise, there was an increase in the average phytoplankton abundance at the stations sampled. Diatoms again were the most abundant group, although the abundance of other groups increased significantly. Isolated large populations of green and blue-green algae were found, although heterocyst-forming blue-greens were still essentially absent. The distribution of flagellates was interesting. Largest abundances were found in the western half of the bay, which was opposite the trend of diatom abundance.

The fourth cruise began 28 April (Fig. 3). Total phytoplankton abundance continued to increase, with the largest proportional increases occurring in the flagellate groups. As had been true during the previous sampling period, there appeared to be an inverse relationship between the abundance of diatoms and flagellates. Green algae began to appear in significant abundance at stations in and near the Saginaw River. The abundance of blue-green algae remained relatively low, and heterocyst-forming taxa were still essentially absent.

The fifth cruise was started 13 May (Fig. 4). Overall phytoplankton abundance continued to increase and extremely large abundances were noted at stations near the mouth of the Saginaw River. All of the major phytoplankton groups were abundant at one or more stations in this region. Flagellates were less abundant at most stations than during the previous cruise, but green and blue-green algae continued to increase. Relatively large populations of heterocyst-forming blue-green algae were found for the first time, particularly at shoreward stations.

The sixth cruise was begun 3 June (Fig. 5). During this cruise, a distinct change in the distribution and abundance of major phytoplankton groups became apparent. Diatoms remained abundant at stations in the vicinity of the Saginaw River, but were generally reduced in abundance at stations in other parts of the bay. It appeared that populations were maintained in this region as a direct result of nutrient resupply from the Saginaw River, while populations in other regions of the bay were becoming nutrient limited. Green and blue-green algae became more important elements of assemblages, particularly at stations in the southern and eastern sectors of the bay. The distributions noted are probably indicative of incipient secondary silica and nitrogen limitation and transport of excess phosphorus along the eastern coast of the bay.

The next cruise was undertaken 17 June (Fig. 6). Sampling during this period showed a substantially different trend in phytoplankton abundance and distribution than the previous sampling round. Phytoplankton abundance generally declined and the distribution of major groups was more erratic than it had been during the previous sampling. Relatively large abundances of total phytoplankton and particularly diatoms and green algae were found at stations in the southeastern sector of the outer bay. It appeared that during this period these populations were being advected from the bay to Lake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GREENS
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BLUE-GREENS W/O
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TOTAL
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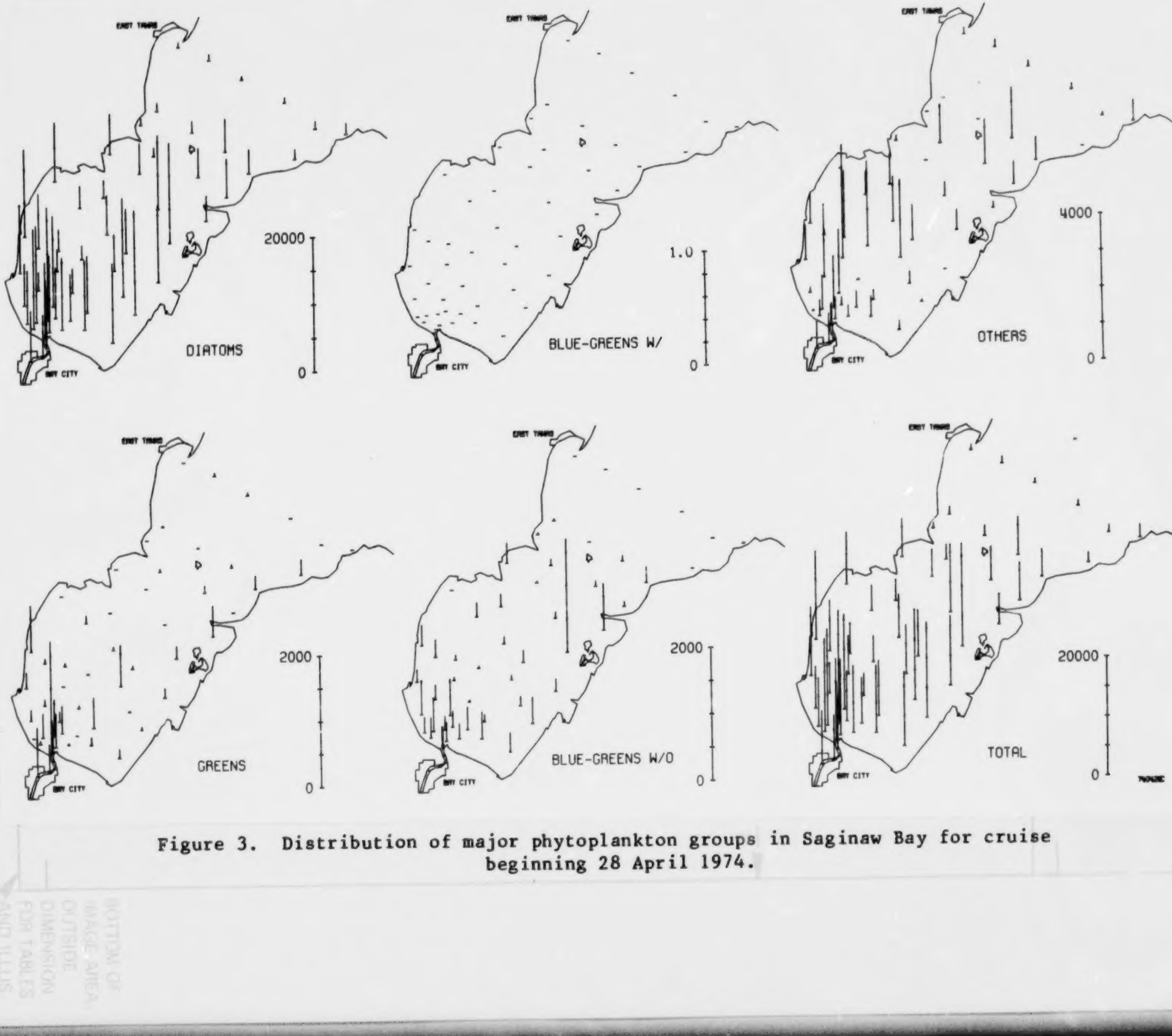
Figure 2. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 6 April 1974.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BLUE-GREENS W/O
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TOTAL
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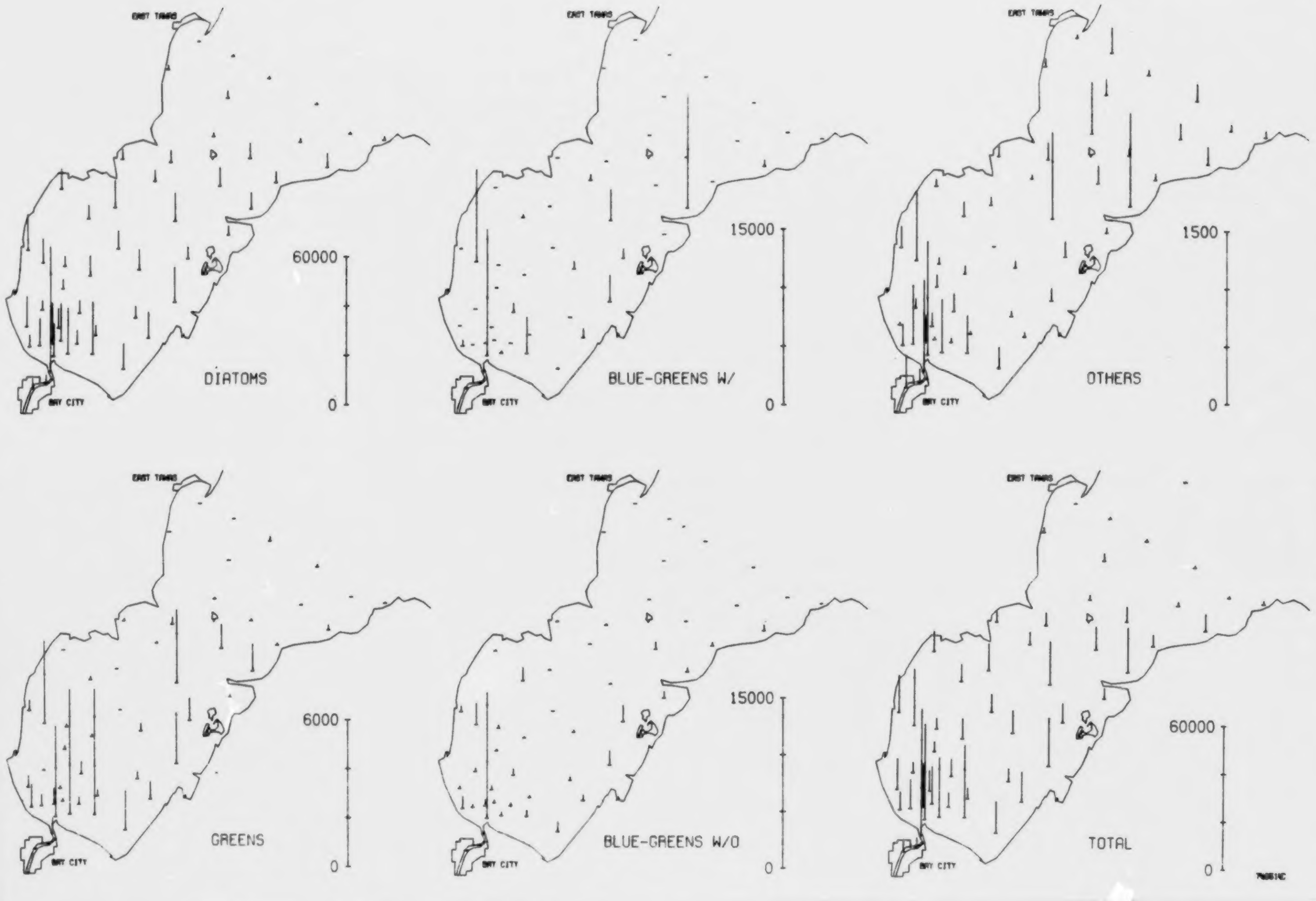
0

Figure 3. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 28 April 1974.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GREENS
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Figure 4. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 13 May 1974.

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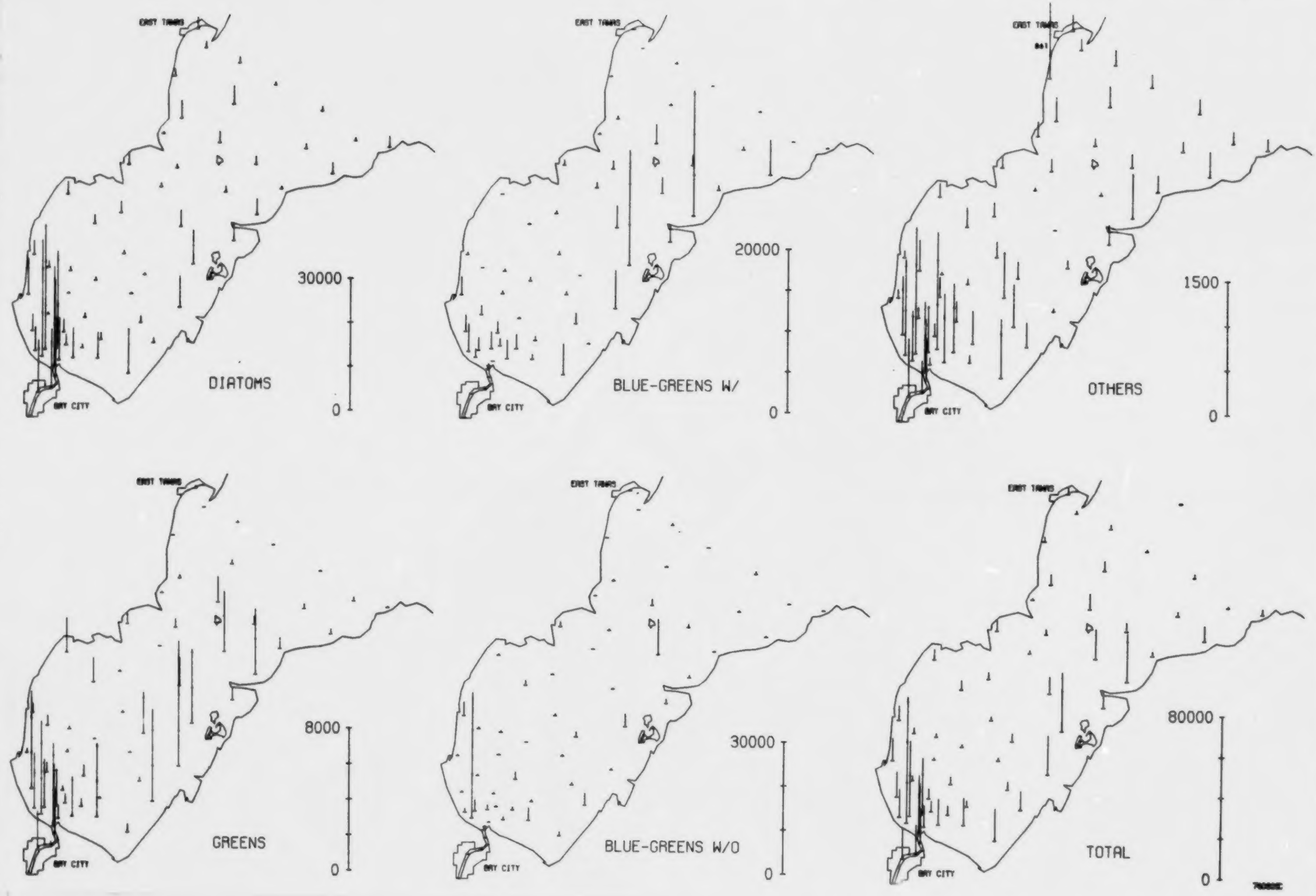
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GREENS
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BLUE-GREENS W/O
30000
0
TOTAL
80000
0

Figure 5. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 3 June 1974.

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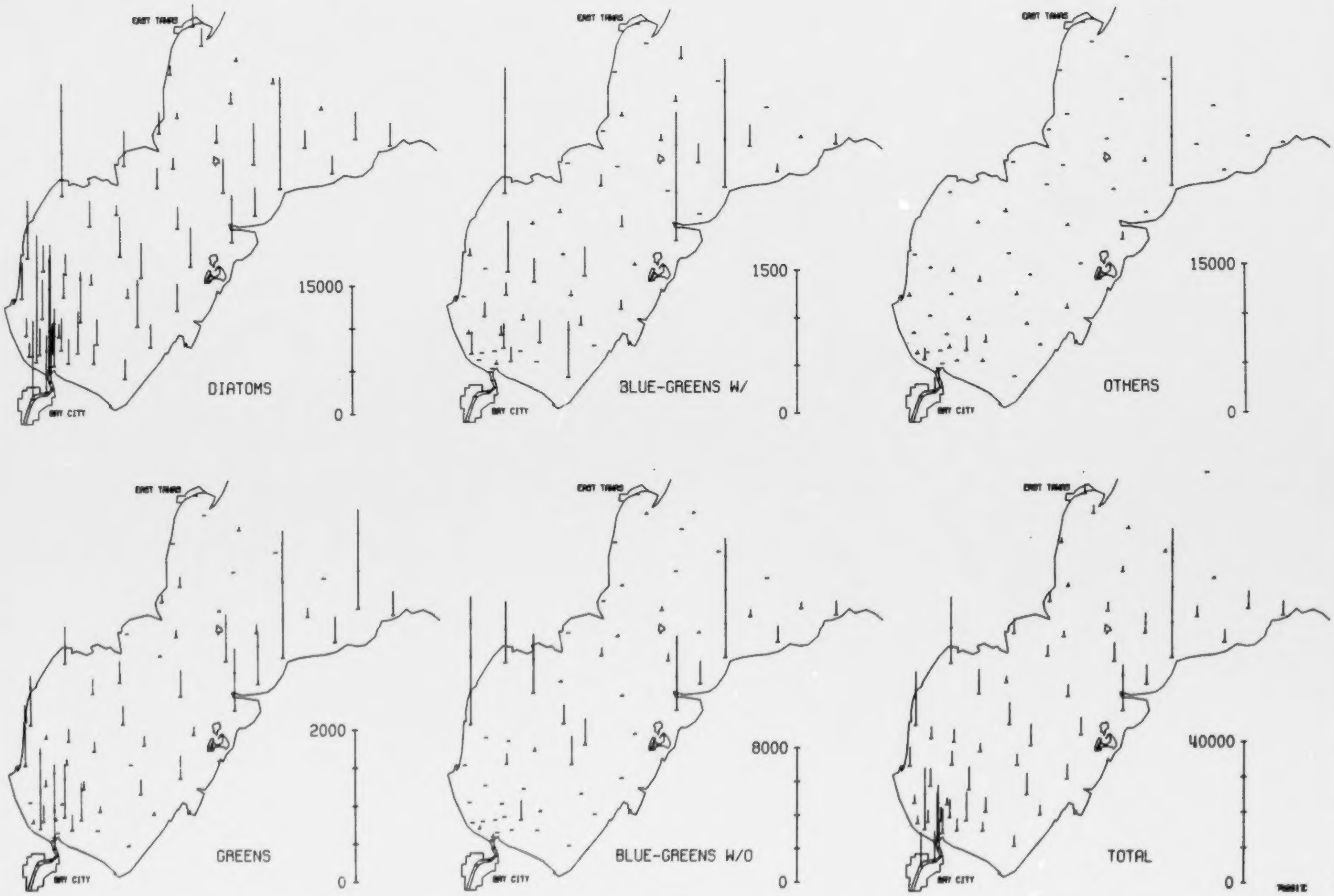
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OTHERS
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GREENS
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BLUE-GREENS W/O
8000
0
TOTAL
40000
0

Figure 6. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 17 June 1974.

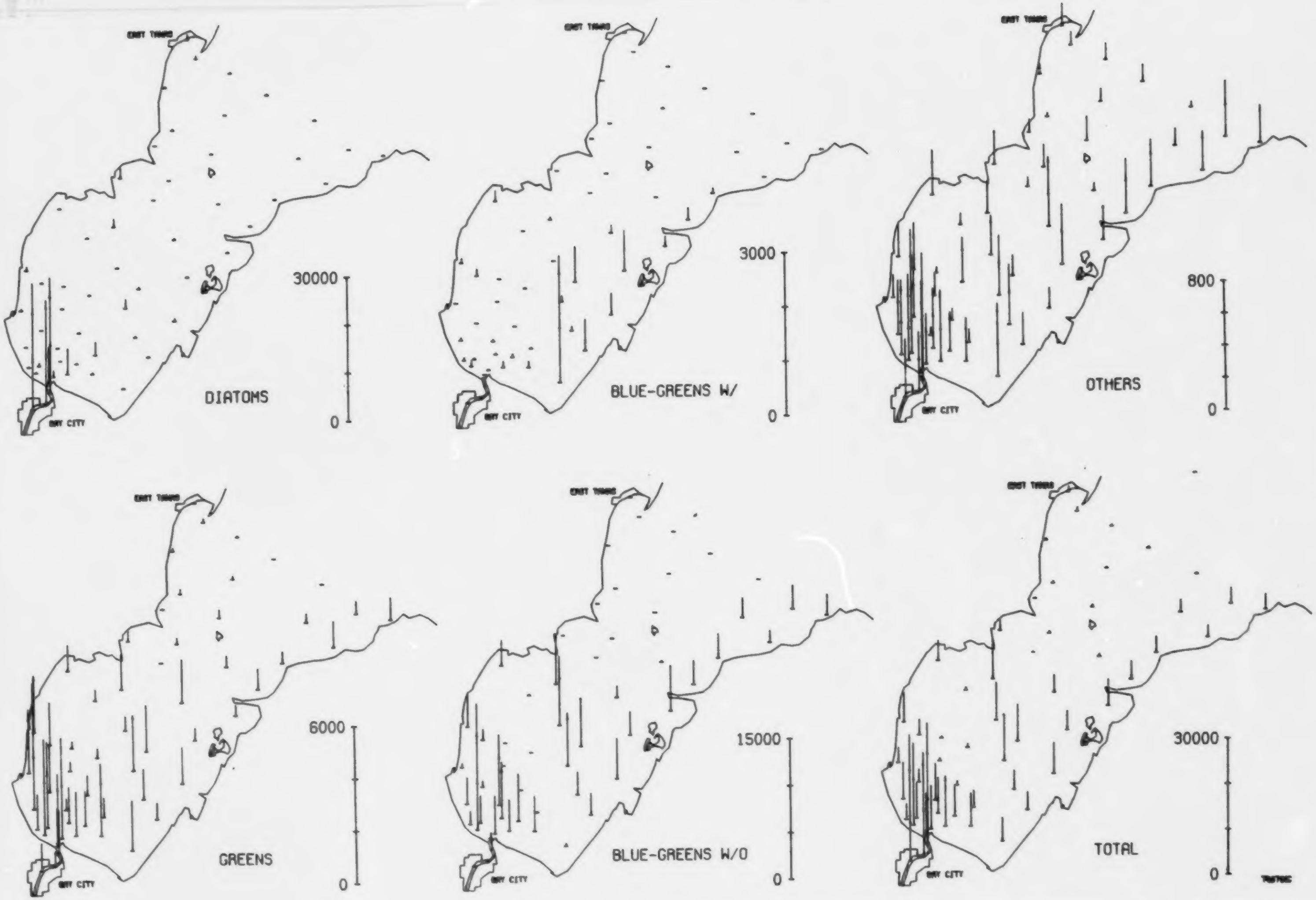
Huron along the southeastern shore. One of the unusual features of this sample set was the extreme abundance of total phytoplankton and all of the major groups at Station 44, near Oak Point. The reason for the atypical abundance at this particular station is not apparent.

Cruise 8 was begun 8 July (Fig. 7). Phytoplankton distribution at this time was quite different than during the previous sampling period. Total phytoplankton abundance declined, and high population densities were restricted mostly to stations in the lower bay and stations along the southeastern shore. The abundance of diatoms declined sharply except at stations in the Saginaw River and immediately adjacent to its mouth. Green and blue-green algae remained relatively abundant, but heterocyst-forming blue-green algae were restricted to stations in the southeastern segment of the area sampled. Relatively low abundance of flagellates was noted at all stations sampled. The most unusual feature of the results from this cruise is the extremely low abundance of phytoplankton in segment 4 of the sampling array. As was the case in the previous set, it appeared that phytoplankton from the lower bay was being transported along the southeastern coast of Saginaw Bay and into Lake Huron.

The next sampling round was undertaken 24 July (Fig. 8). Phytoplankton distribution during this sampling period was again markedly different than it had been during the previous sampling interval. Total abundance increased somewhat, but abundance consistently declined along the long axis of the bay and there was no evidence of particularly high abundance along the southern shore, as there had been previously. Stations along the Lake Huron interface and most stations in segment 5 had very low phytoplankton abundance. Large populations of diatoms and heterocyst-forming blue-green algae were restricted to stations near the mouth of the Saginaw River. Large populations of diatoms were found at stations in the river, but blue-greens were not particularly abundant except in the bay.

The next sampling cruise began 25 August (Fig. 9). By this time the total abundance of phytoplankton had generally decreased. Assemblages were dominated by blue-green algae, although the abundance of diatoms had recovered slightly from the levels observed during the previous cruise. Population distributions of all groups was rather uniform, with a decrease in abundance from the lower bay to the Lake Huron interface. During this cruise, greatest phytoplankton abundance occurred at Station 50, the central station on the Lake Huron interface, rather than at shoreward stations as had been the general case previously. Flagellate numbers were very low during this cruise and the largest populations were found in the lower bay.

A further decline in peak phytoplankton abundance was noted during the next sampling cruise, which began 18 September (Fig. 10). Relatively high levels of total phytoplankton standing crop extended further toward the Lake Huron interface however, particularly at stations along the southeastern shore. The flora was dominated by blue-green algae, particularly taxa which do not form heterocysts. Significant populations of heterocyst-forming species were restricted to stations immediately along the southeast shore. Diatoms were most abundant in the Saginaw River, but significant populations were present at most stations sampled. Diatoms increased in abundance at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GREENS
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BLUE-GREENS W/O
15000
0
TOTAL
30000
0

Figure 7. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 8 July 1974.

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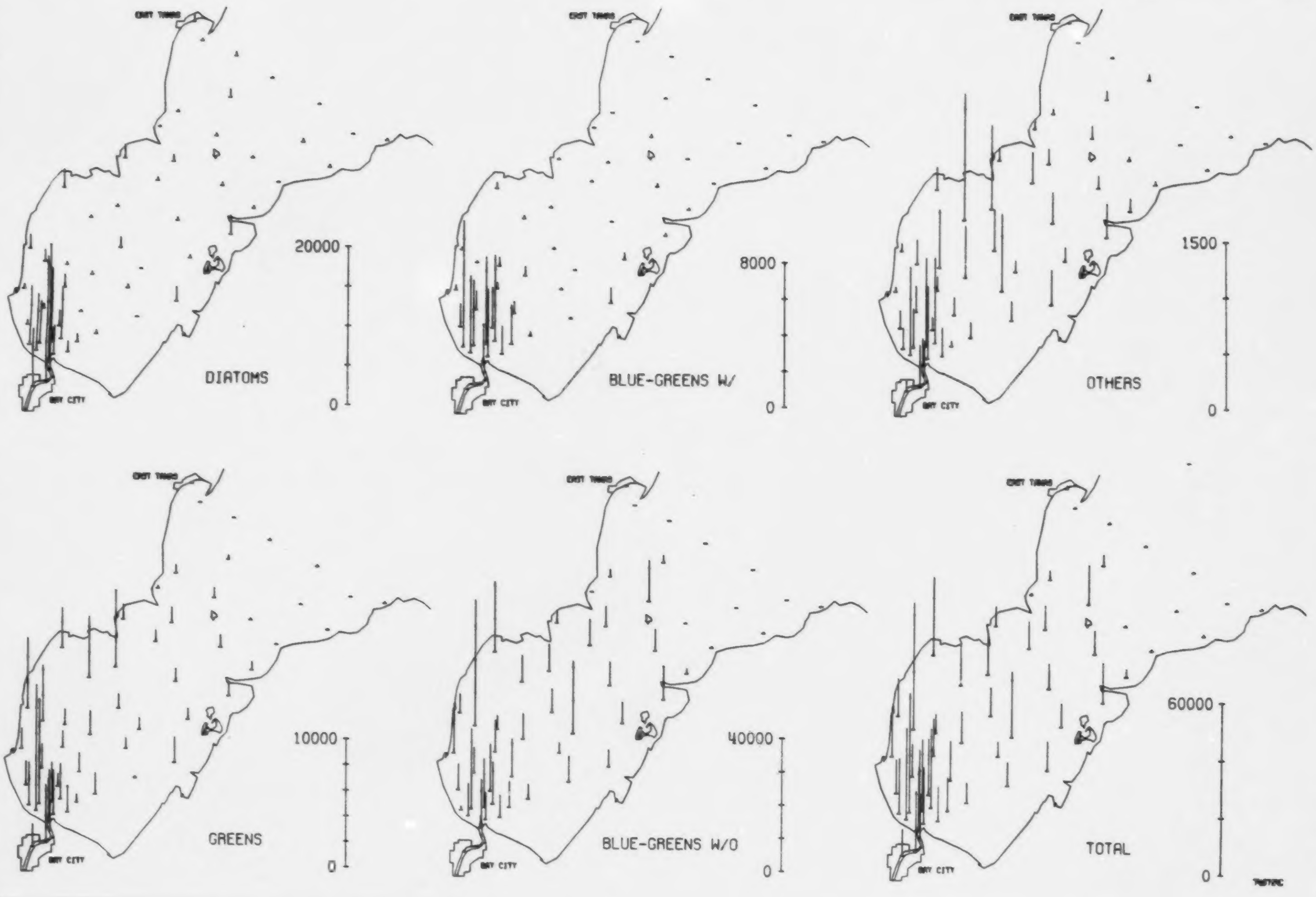
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TOTAL
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Figure 8. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 24 July 1974.

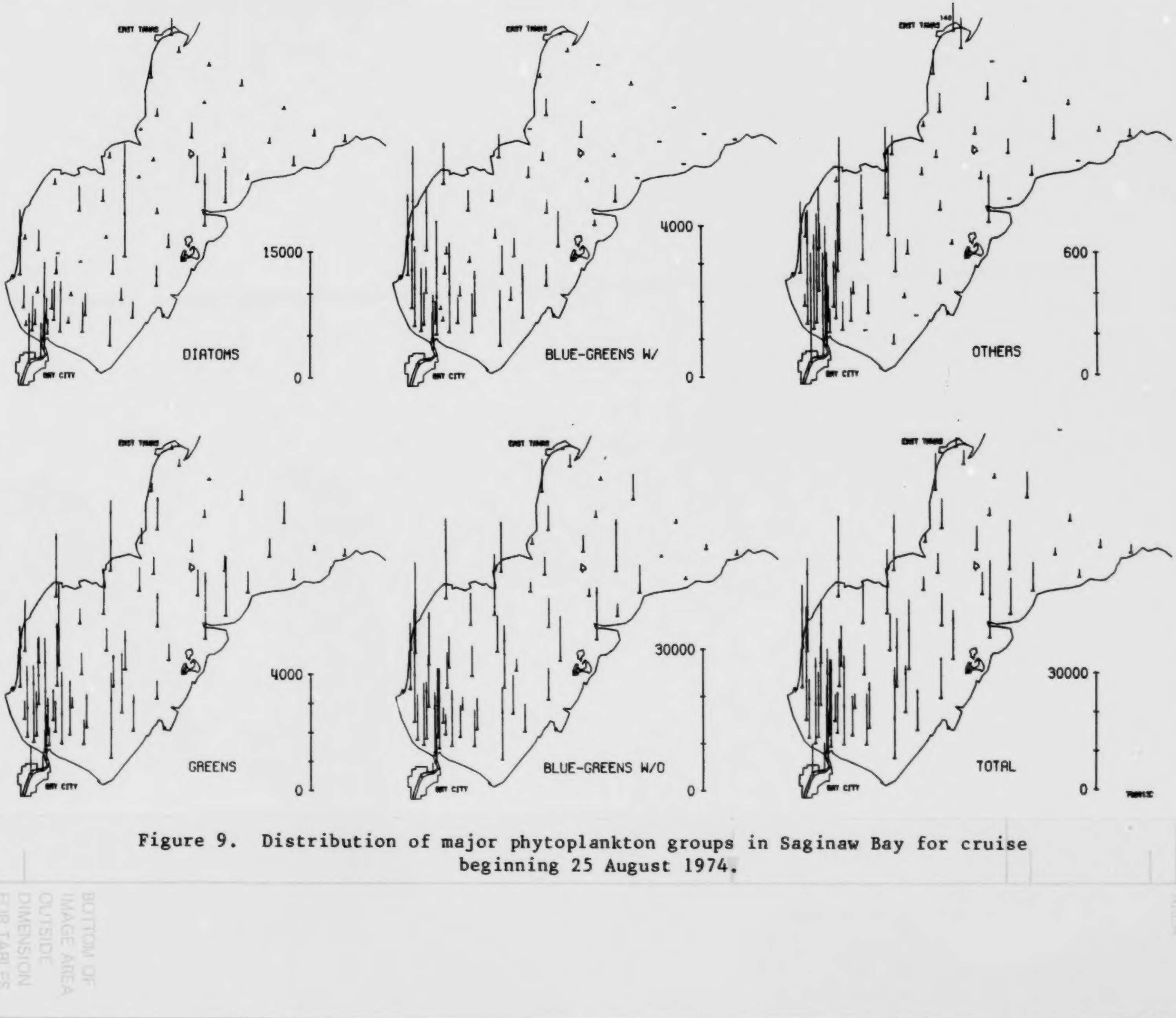
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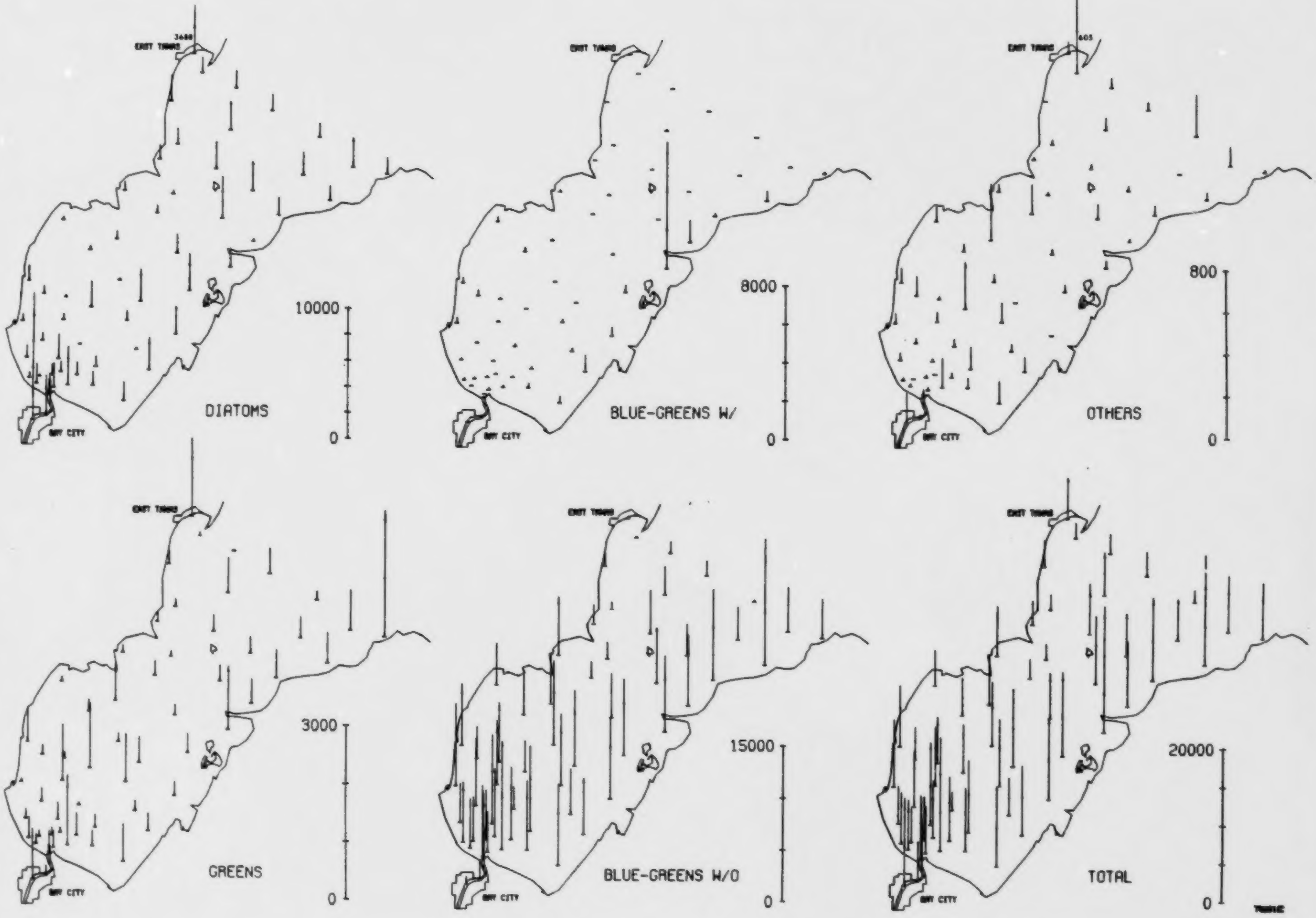
Figure 9. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 25 August 1974.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BLUE-GREENS W/O
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0
TOTAL
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0

Figure 10. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 18 September 1974.

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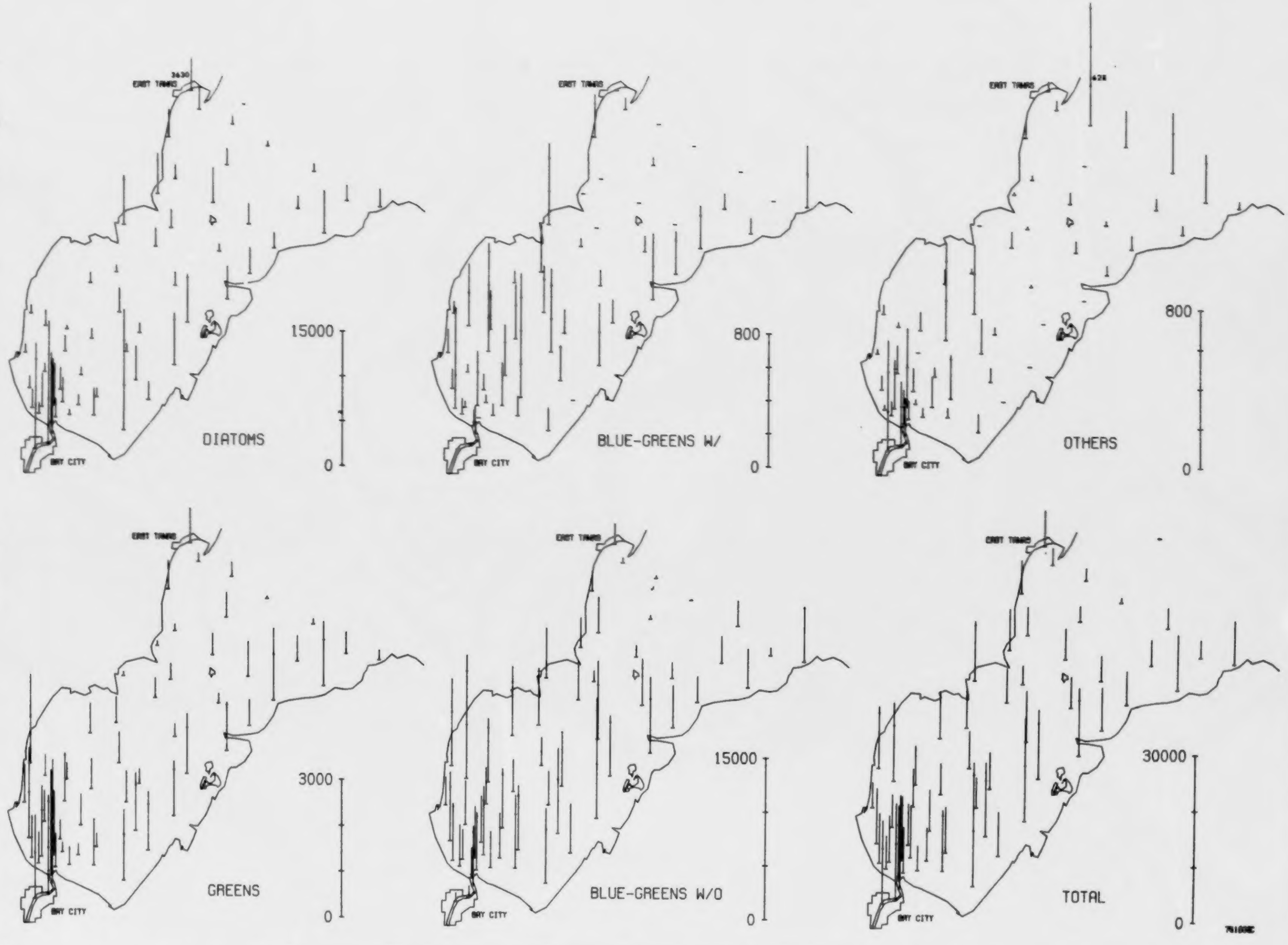
stations in the Lake Huron interface, but the assemblage in this region contained a completely different suite of populations than was present in the Saginaw River or in the lower bay. Green algae were a relatively important part of assemblages sampled at most stations. Unusually high numbers of diatoms, green algae, and flagellates occurred at Stations 47 and 48 in Tawas Bay.

The next sampling cruise was delayed until 6 October (Fig. 11). By this time the general level of phytoplankton standing crop had increased somewhat in most areas of the bay. Blue-green algae remained the dominant element of the flora, but diatoms had increased significantly in abundance, particularly at nearshore stations. Heterocyst-forming blue-green algae were less abundant than during the previous sampling period, but populations were present at most stations sampled. Green algae remained important at most stations sampled and they, together with diatoms and flagellates, were the most important components of the Saginaw River flora as it entered the bay. The relative abundance of flagellates was also high at stations in the Lake Huron interface, although a different suite of species was present there than in the river and lower bay.

The next samples were taken 11 November (Fig. 12). Although less than complete sampling was achieved, a reasonably complete reconstruction of phytoplankton distribution within the bay can be made. Total phytoplankton standing crop decreased significantly from levels of the previous month. Diatoms were the dominant element at most stations sampled, although blue-green algae remained abundant, particularly at nearshore stations and stations in the lower bay. The abundance of heterocyst-forming taxa was much reduced and only small populations were found at scattered stations. Green algae and flagellates were relatively minor elements of assemblages at stations sampled. In the lower bay there appeared to be an inverse relationship between the abundance of these two groups.

Only a very limited number of stations in the lower bay and in the Saginaw River were sampled on 16 December (Fig. 13). Somewhat surprisingly, the total abundance of phytoplankton at the stations sampled was relatively high. The flora was dominated by diatoms, with a minor and approximately equal contribution of blue-green algae and flagellates. Unlike previous samples, flagellates were most abundant in samples from the Saginaw River. Green algae were present, in low abundance, at most stations sampled, but heterocyst-forming blue-green taxa were not noted in this set of samples.

A similarly small number of stations in the lower bay were sampled on 20 February 1975 (Fig. 14). Surprisingly high total phytoplankton abundance was found at a series of stations in the western half of segment 1. Diatoms dominated the flora in this region and in total. Flagellates were relatively abundant at a number of nearshore stations sampled. Significant quantities of green algae were found only at Station 59, although a few specimens of species in this group were noted at most stations sampled. Blue-green algae were virtually absent, although a small population of *Oscillatoria* was found at Station 14.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BAY CITY
OTHERS
800
0
EAST TAWAS
BAY CITY
GREENS
3000
0
EAST TAWAS
BAY CITY
BLUE-GREENS W/O
15000
0
EAST TAWAS
BAY CITY
TOTAL
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0
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Figure 11. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 6 October 1974.

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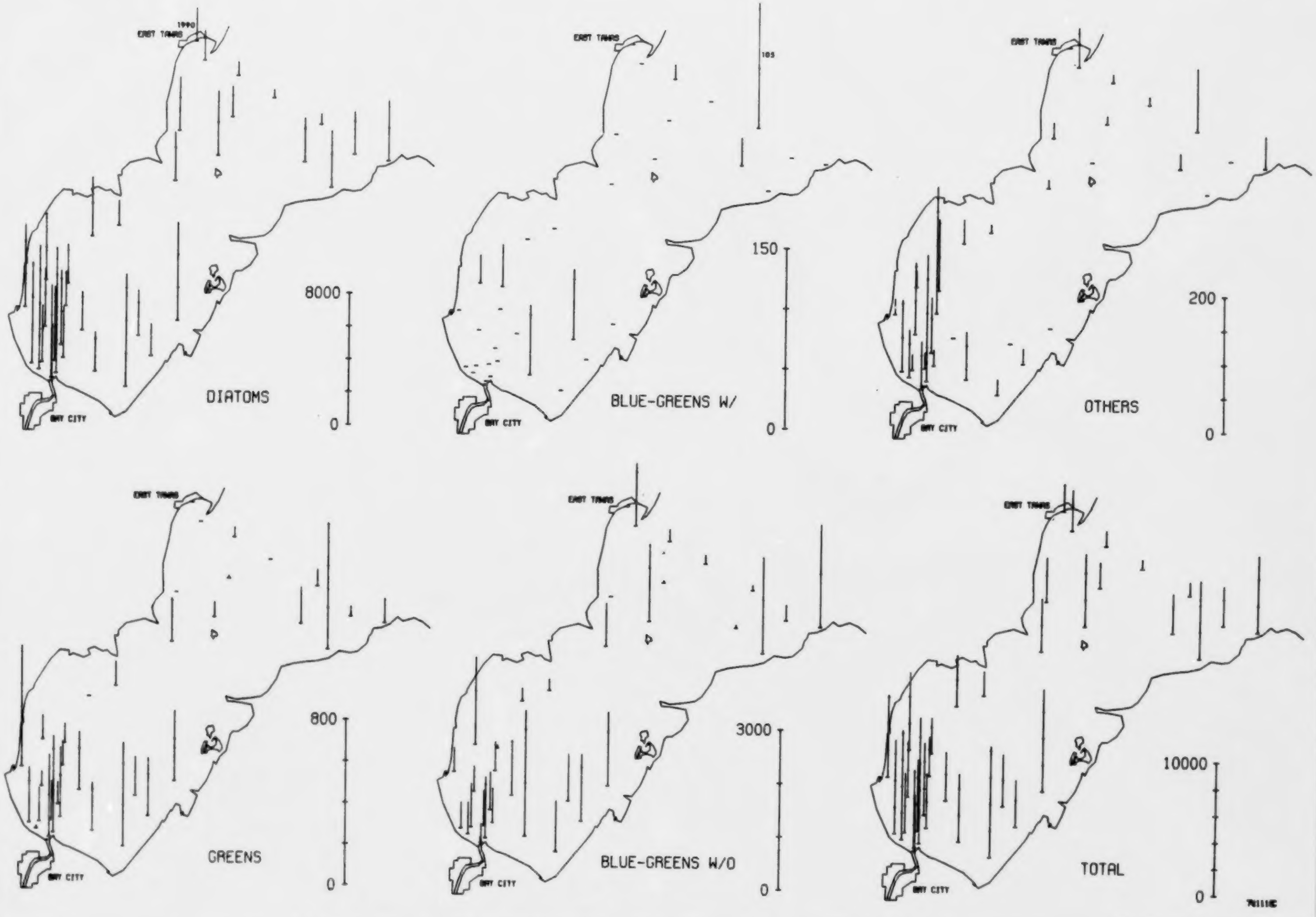
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OTHERS
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BAY CITY
EAST TAWAS
GREENS
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BAY CITY
EAST TAWAS
BLUE-GREENS W/O
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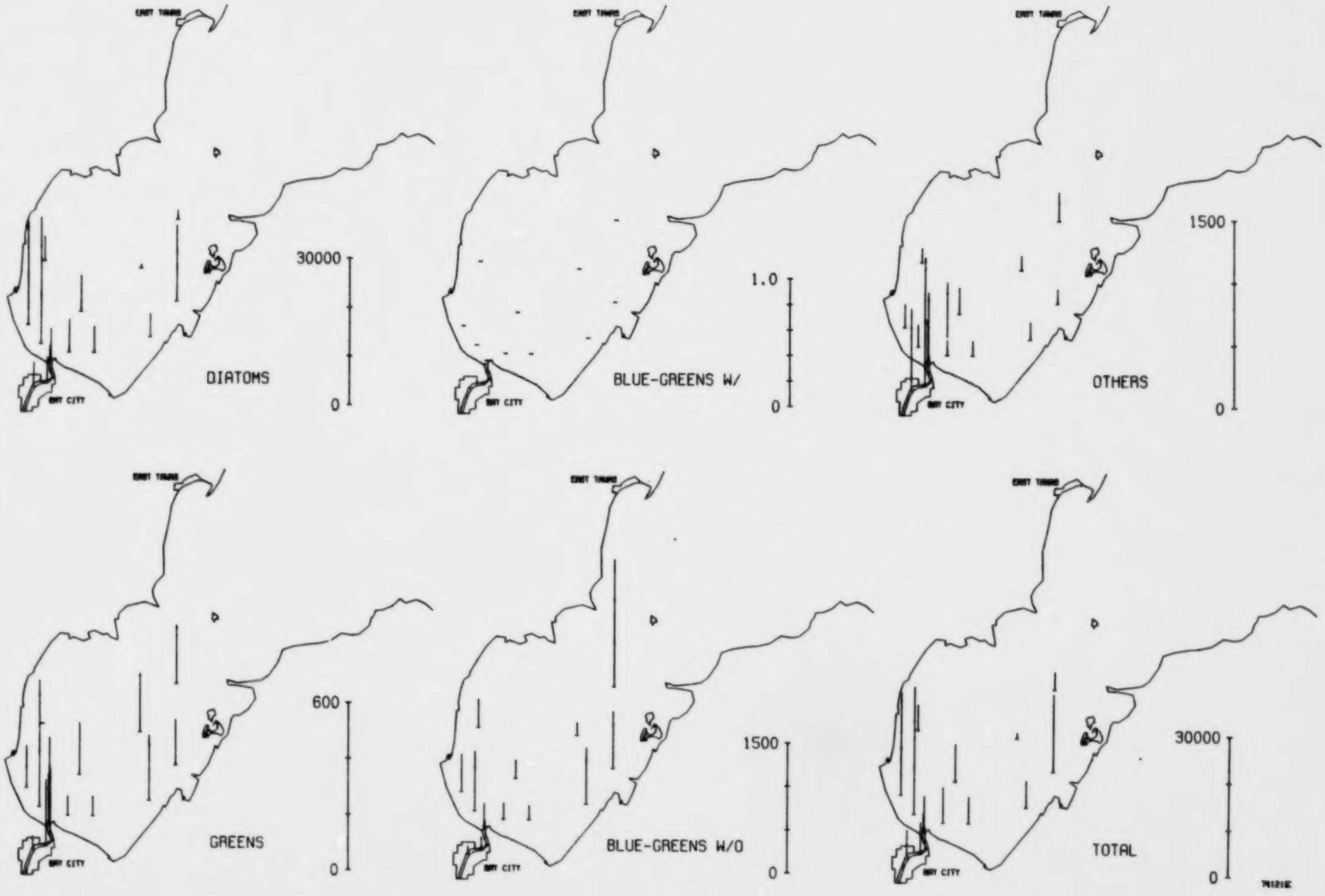
0
BAY CITY

Figure 12. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 11 November 1974.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GREENS
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BLUE-GREENS W/O
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0
TOTAL
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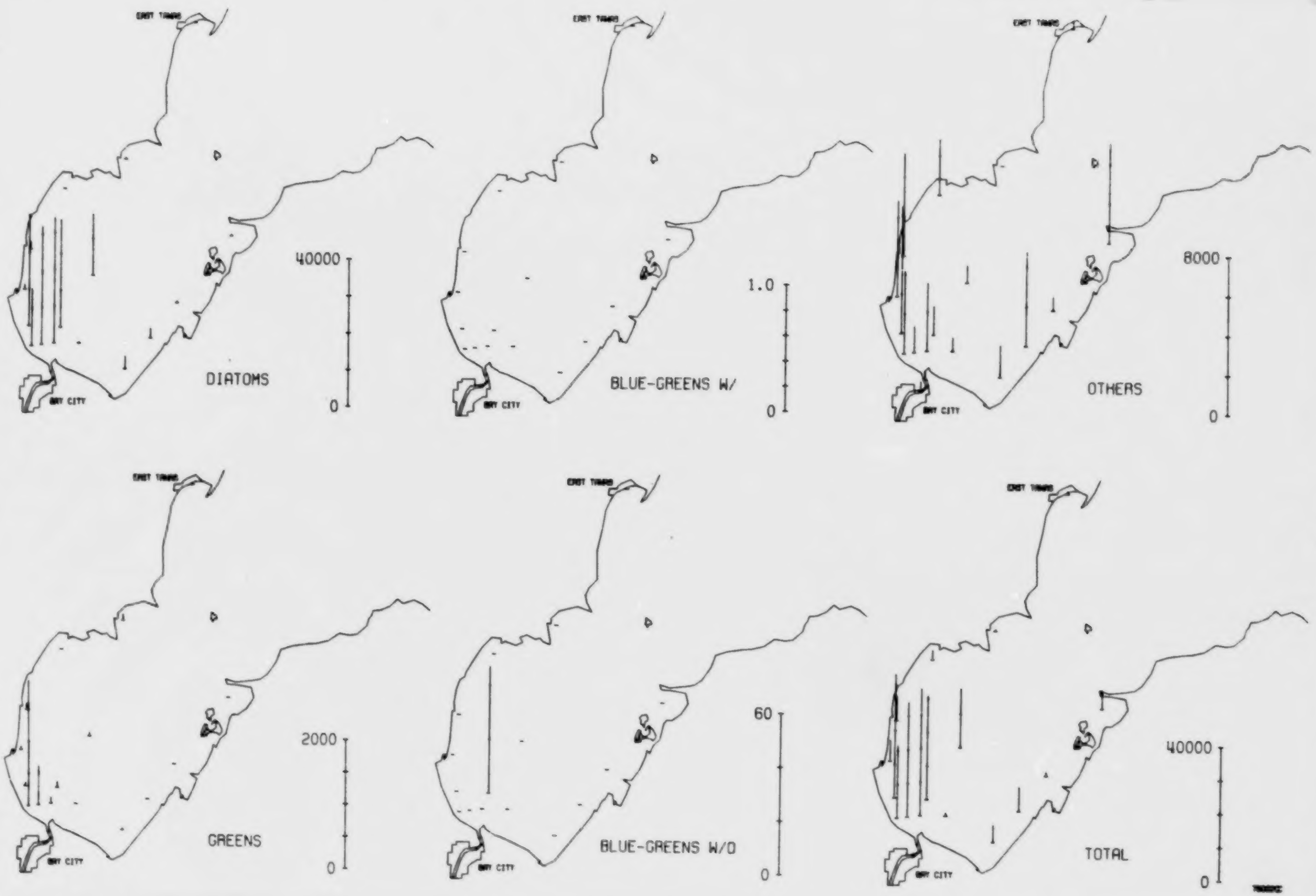
0

Figure 13. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 16 December 1974.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GREENS
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0
BLUE-GREENS W/O
60
0
TOTAL
40000
0

Figure 14. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 20 February 1975.

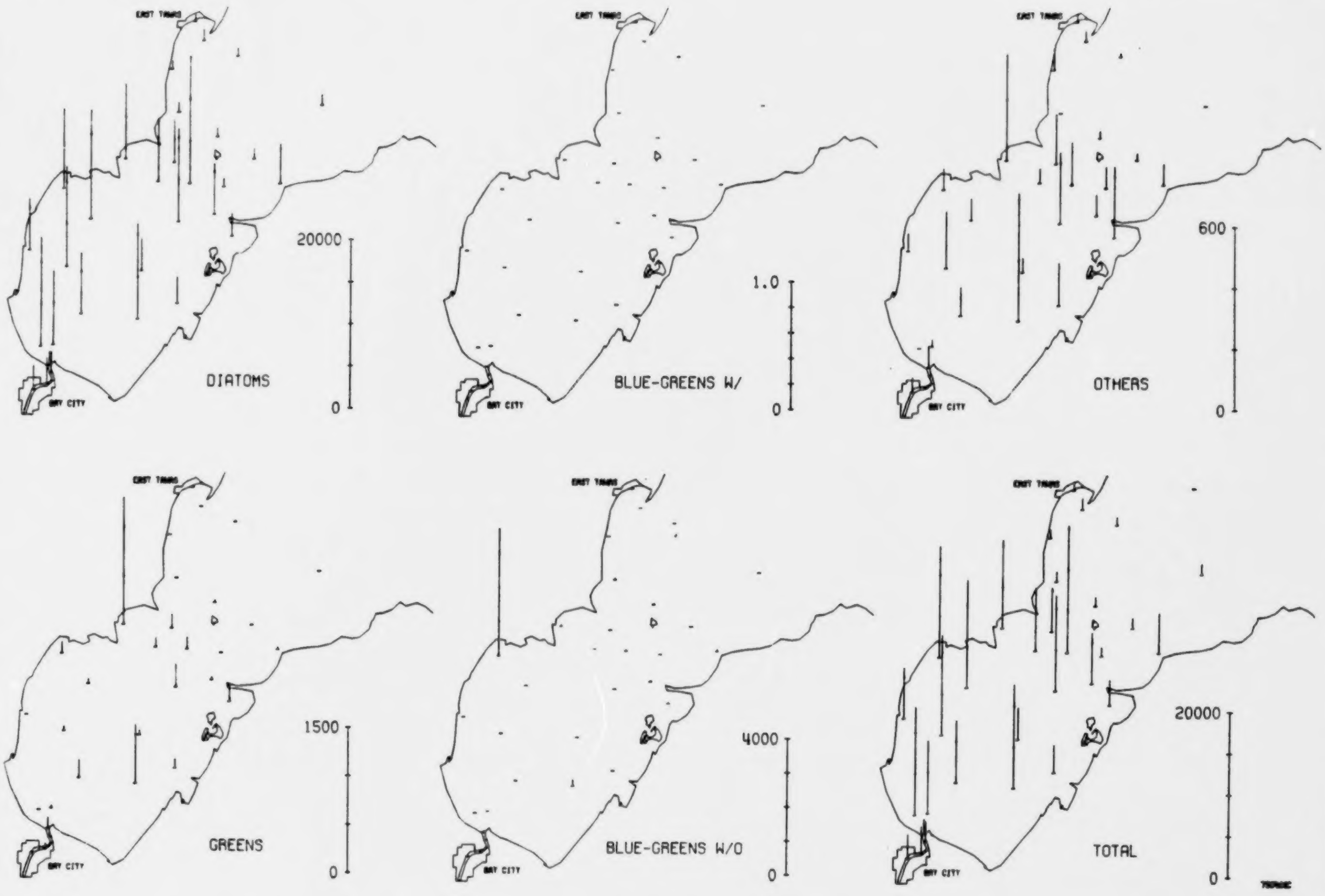
A more comprehensive set of samples was obtained on a cruise beginning 8 April (Fig. 15). Although the maximum abundance was significantly reduced from the levels noted during the previous sampling period, relatively high levels of phytoplankton standing crop were found at stations in the inner bay. During this period the flora was completely dominated by diatoms, although green algae and flagellates were found in most assemblages sampled. Blue-green algae were not present in significant abundance except at Station 30.

The next cruise in the sequence was undertaken 28 April (Fig. 16). Total phytoplankton abundance had increased from levels of the previous month. The flora was still dominated by diatoms, but increasing quantities of green and blue-green algae were present, particularly at stations in the lower bay and along the eastern shore. Heterocyst-forming blue-greens were still virtually absent at all stations sampled. Flagellates were present in moderate abundance and representatives of this group were generally distributed at the stations sampled.

By the time the next cruise was undertaken on 20 May (Fig. 17), maximum levels of phytoplankton abundance in the bay had decreased somewhat. Unlike the previous month, however, relatively high levels of abundance were found at shoreward stations in the Lake Huron interface area. This increase was accounted for mostly by diatoms, which remained the most abundant component of the flora. Diatoms were abundant in the Saginaw River and at most stations in the bay. Green and blue-green algae, on the other hand, were abundant only at stations in the inner bay. Green algae were particularly abundant at a series of stations just off the mouth of the Saginaw River. Somewhat atypically, flagellates were abundant in the Saginaw River and adjacent stations, although certain populations were present at all stations sampled.

The number of stations sampled was reduced during the next cruise, which began 5 June (Fig. 18). At this time there was an extreme variance in phytoplankton abundance among the stations sampled. This was exemplified by a very high abundance of blue-green algae at Station 34 in Wild Fowl Bay. Diatoms remained, overall, the most abundant of the major groups. Their abundance at the stations sampled was quite variable. Atypically high abundance was found at Station 36, near the mouth of the Au Gres River. Green and blue-green algae continued to increase in abundance, particularly at stations in segments 1 and 3 of the sampling array. Representatives of the flagellate groups remained most abundant at stations in the lower bay.

The next sampling cruise began 25 June (Fig. 19). By this time total phytoplankton abundance had been somewhat reduced at most open-water stations, although high total numbers were found at a number of nearshore stations. The abundance of diatoms was much reduced, except at stations in and near the Saginaw River and at nearshore Stations 36 and 53. Green and blue-green algae were abundant at most stations in the lower bay and a particularly high abundance of this group was again noted at Station 34, in Wild Fowl Bay. Flagellates remained abundant and were somewhat more generally distributed than was the case in the previous cruise.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GREENS
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TOTAL
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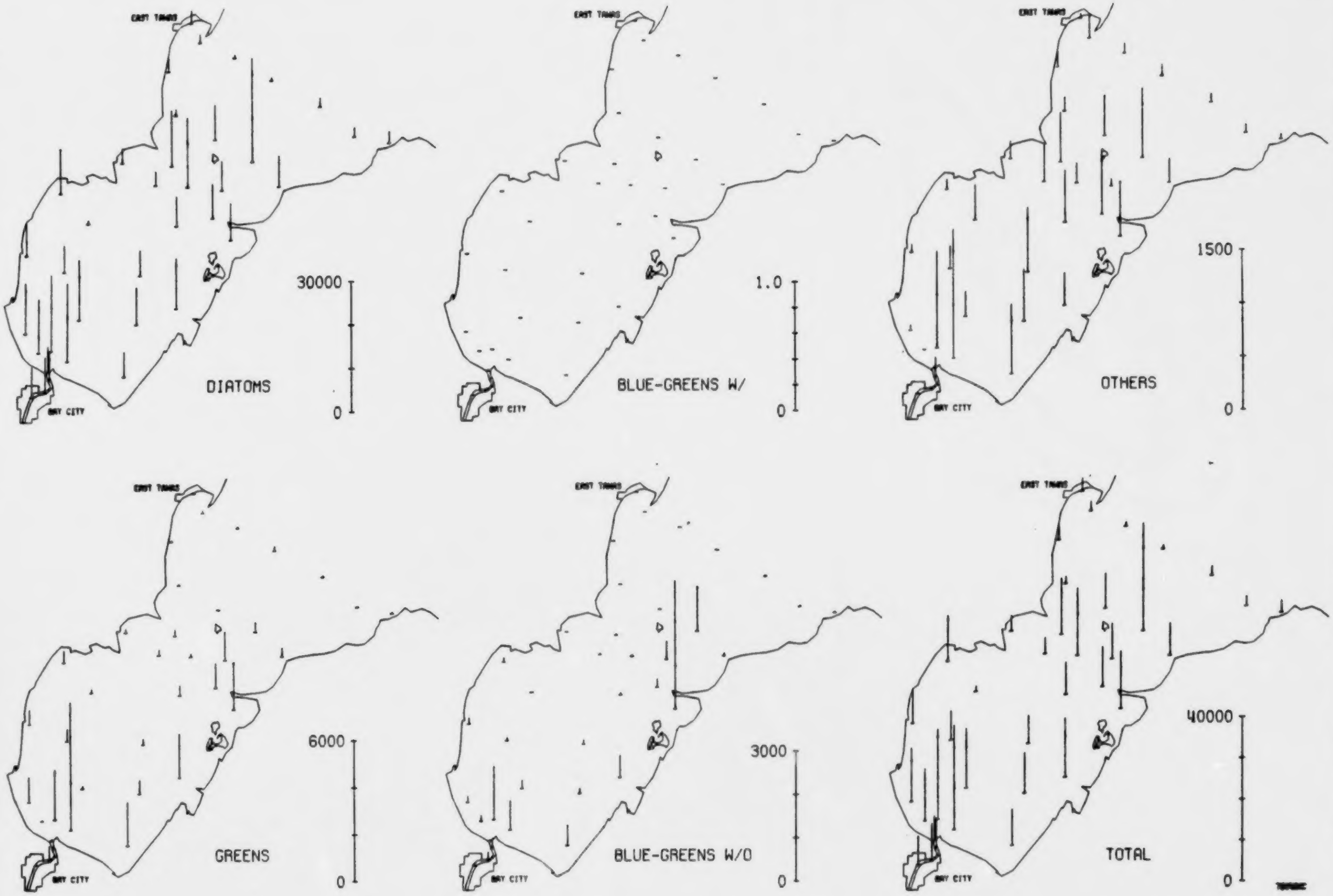
Figure 15. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 8 April 1975.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TOTAL
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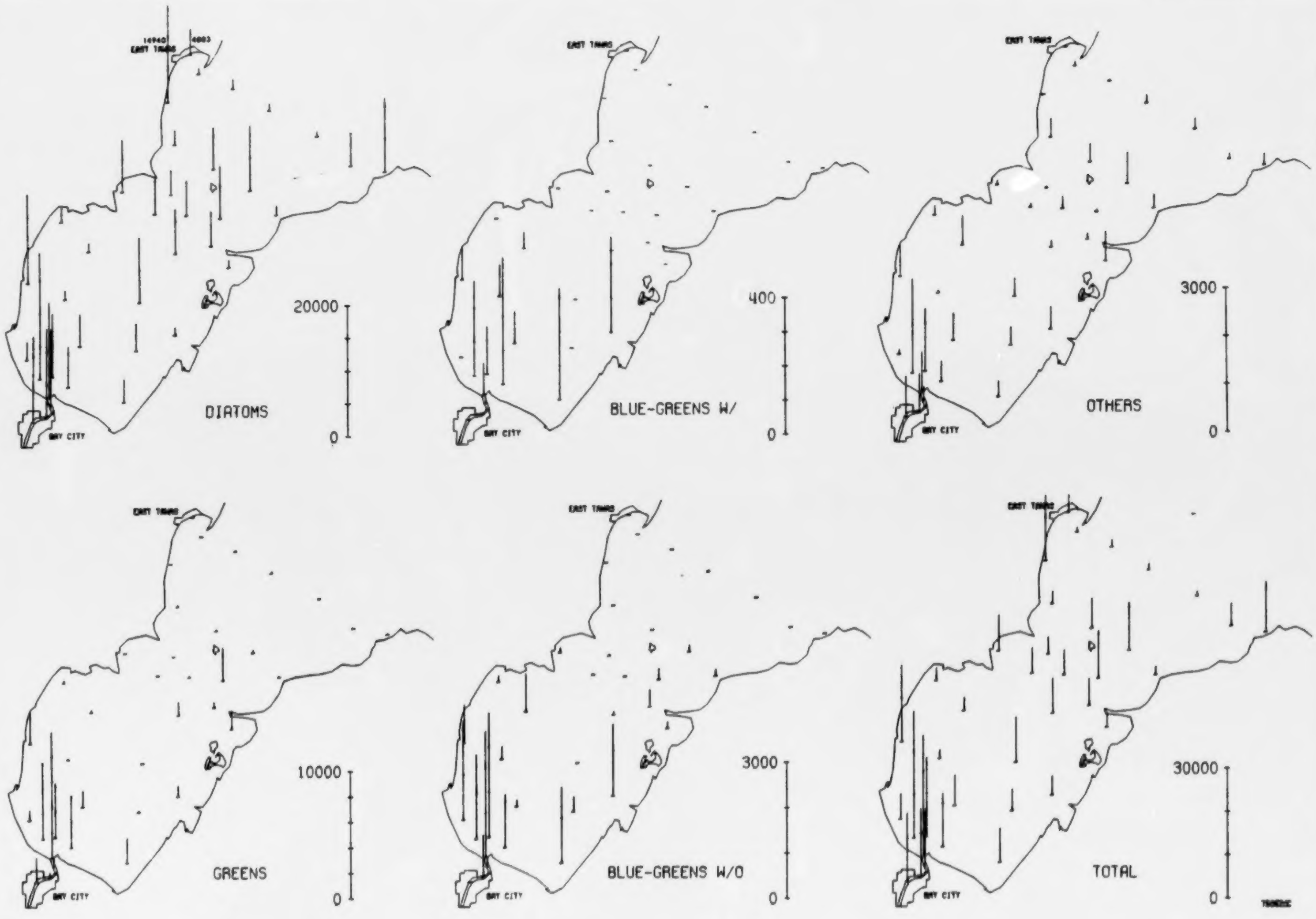
Figure 16. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 28 April 1975.



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GREENS
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TOTAL
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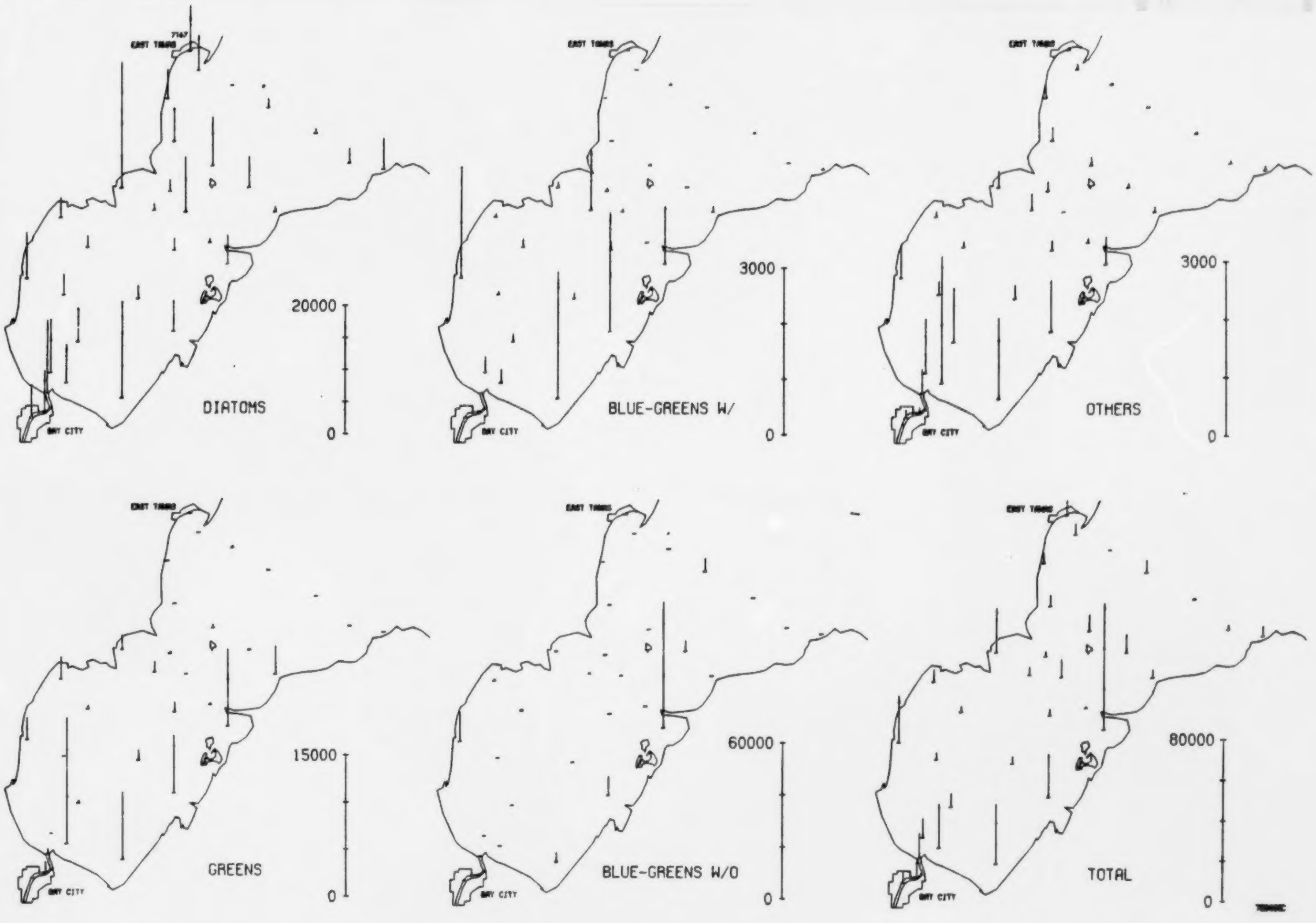
Figure 17. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 20 May 1975.



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OTHERS
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BLUE-GREENS W/O
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TOTAL
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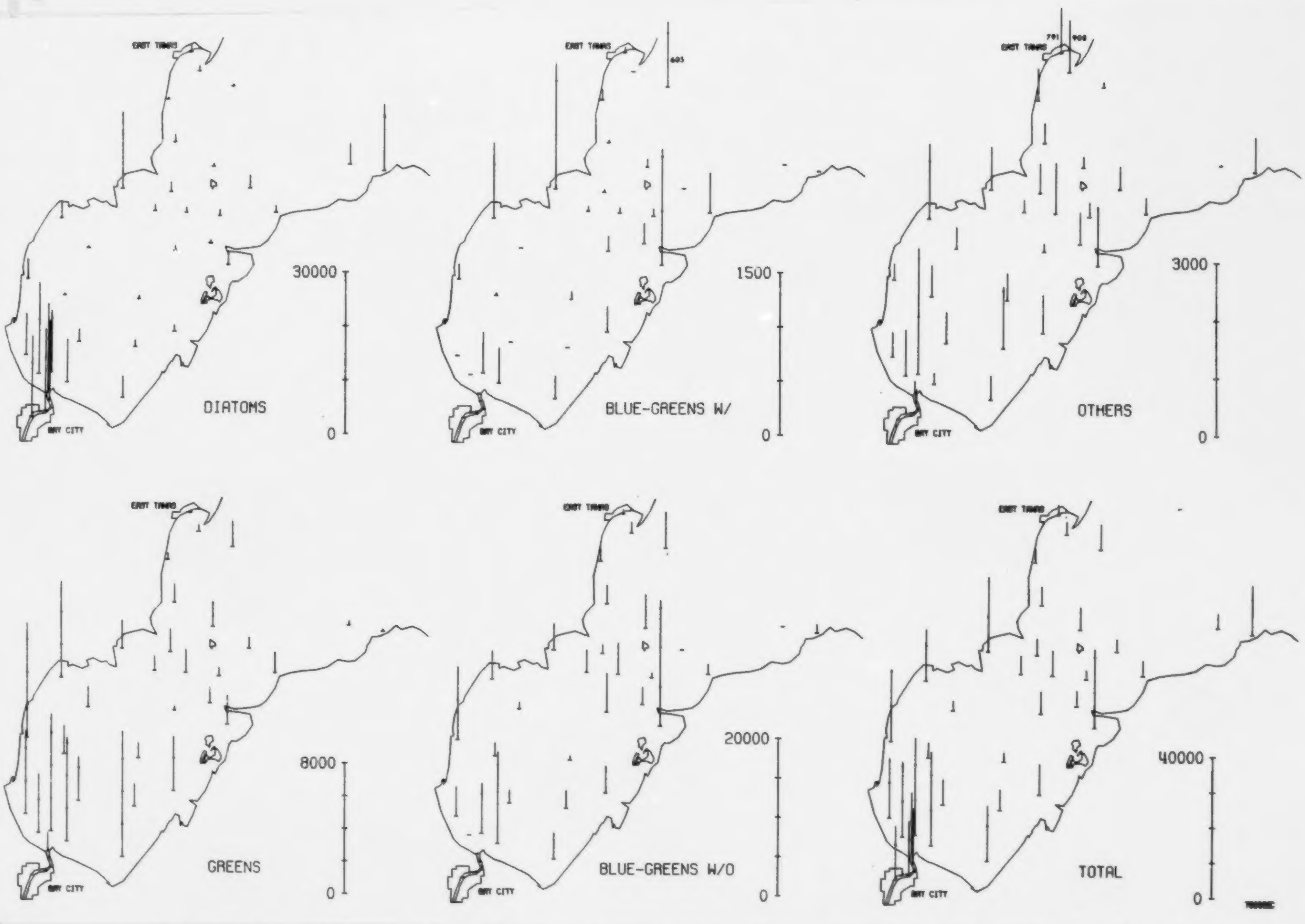
0

Figure 18. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 5 June 1975.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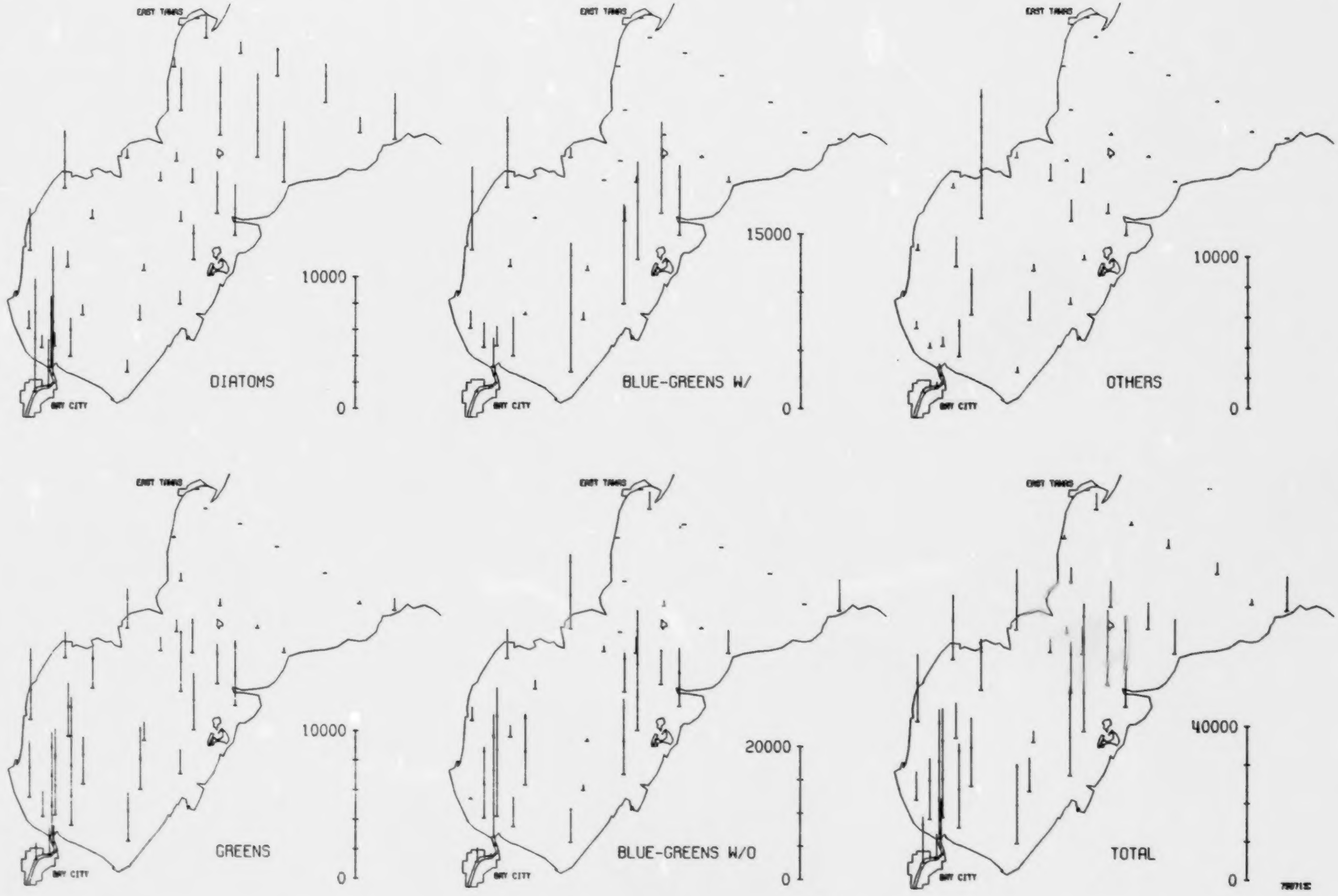
GREENS
8000
0
BLUE-GREENS W/O
20000
0
TOTAL
40000
0

Figure 19. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 25 June 1975.

During the next cruise, which began 11 July, there was a rather striking floristic differentiation between the inner and outer segments of the bay (Fig. 20). During this sampling period total phytoplankton abundance was markedly lower at stations southwest of Charity Island than in the outer bay. This trend is accentuated in some of the major phytoplankton groups. Diatoms were a relatively minor element of the flora during this cruise and there are two regions of greatest abundance. One is in the Saginaw River and immediately adjacent stations. The other is in the outer bay. The species composition of these two regions is almost entirely different. In the other major groups high abundance is restricted to stations in the lower bay. Green algae are abundant during this sampling period and are generally distributed at stations in the lower bay. The blue-green algae were the dominant element of the flora in terms of peak abundance, but high numbers, particularly of heterocyst-forming taxa, were more restricted to nearshore areas. The occurrence of blue-green algae at Stations 44 and 53, along the southern coast, indicates that these populations may have been transported toward Lake Huron by shoreline drift. With the exception of one station, the flagellates constitute a relatively minor fraction of the flora and the populations present are largely restricted to the lower bay.

The next series of samples was taken beginning 29 July (Fig. 21). Although total phytoplankton abundance had increased substantially by the time these samples were taken, distribution of the major groups was somewhat similar to that observed during the previous cruise. The abundance and distribution of diatoms was even more strikingly disjunct than it had been the previous month. Relatively high abundance was found in the Saginaw River and at stations in segment 4, but the abundance of this group was low in the rest of the bay. As was the case the previous month, different species occupied the two regions of maximum abundance. Although green algae were not as abundant as diatoms, significant populations were present at most stations in the lower bay and at Stations 43 and 44 and 52 and 53 along the southern shore of the outer bay. The distribution of blue-green algae was somewhat irregular during this sampling period, but very large abundances were found at some stations. Their distribution followed the same general pattern as the green algae, although large populations of heterocyst-forming species were found only at shoreward stations along the southern coast of the bay. Flagellates were present in relatively low abundance and the populations present were remarkably evenly distributed. Relatively high abundance of organisms in this group was found at stations in the Saginaw River.

The next cruise in this sequence began 18 August (Fig. 22). Maximum total phytoplankton abundance declined from levels observed during the previous sampling period. Greatest total phytoplankton density as found at stations in segments 3 and 5, along the southeastern coast of the bay. Blue-green algae were the dominant element of the flora at this time and were particularly abundant in this region. The distribution of green algae was somewhat more uniform, and sizable populations of representatives of this group were found at most stations in the lower bay. Highest green algal abundance occurred at stations just off the mouth of the Saginaw River. The abundance of diatoms was more uniform than it had been the previous month, but there was still a large difference in the species composition of different areas. Populations in the outer bay were mostly oligotrophic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TOTAL
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0
750711C

Figure 20. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 11 July 1975.

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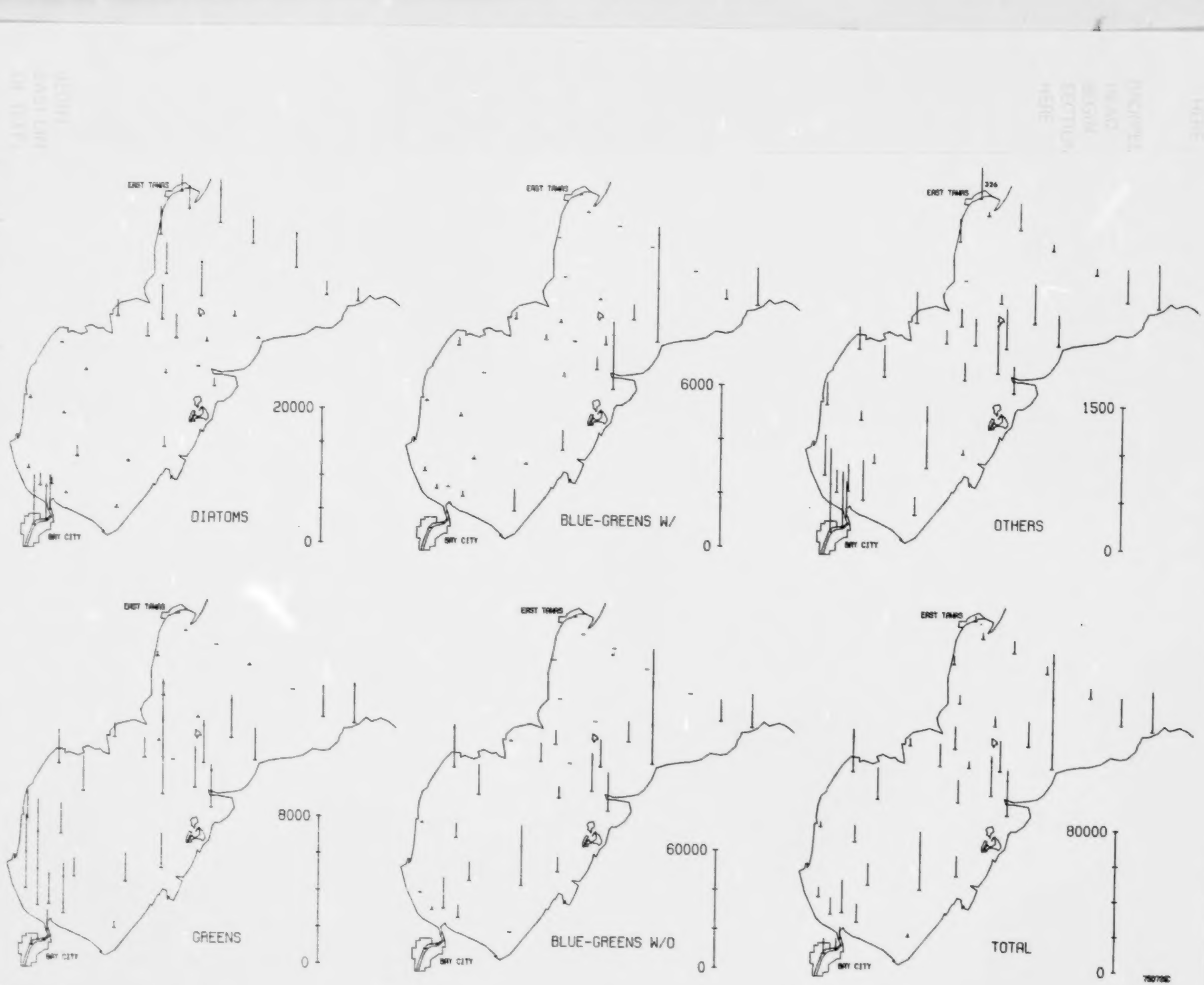
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0
336
OTHERS
1500
0
GREENS
8000
0
BLUE-GREENS W/O
60000
0
TOTAL
80000
0
750780E

Figure 21. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 29 July 1975.

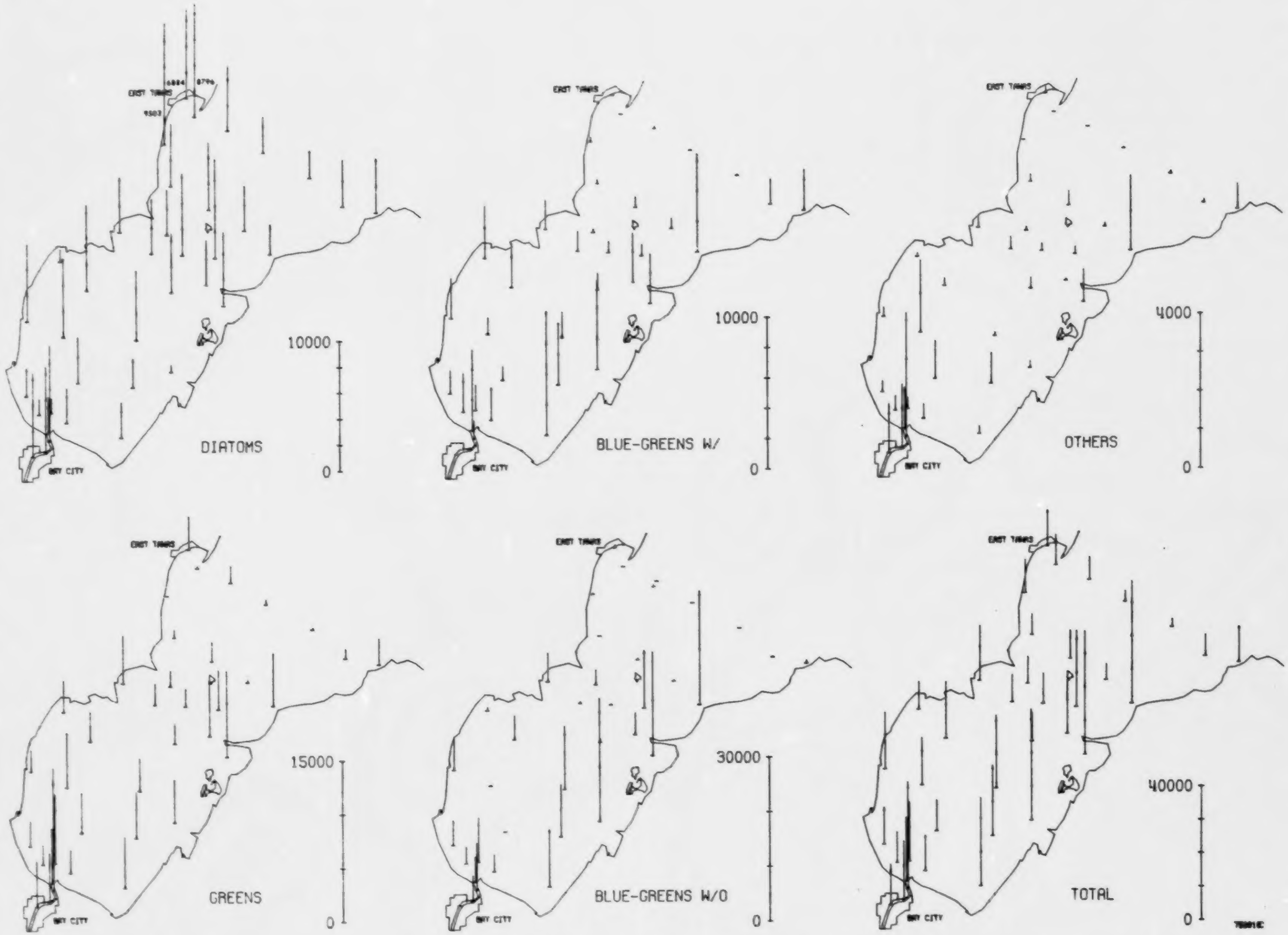

DIATOMS
10000
0
EAST TAWAS
6884
8796
9503
BAY CITY
BLUE-GREENS W/
10000
0
EAST TAWAS
BAY CITY
OTHERS
4000
0
EAST TAWAS
BAY CITY
GREENS
15000
0
EAST TAWAS
BAY CITY
BLUE-GREENS W/O
30000
0
EAST TAWAS
BAY CITY
TOTAL
40000
0
EAST TAWAS
BAY CITY

Figure 22. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 18 August 1975.

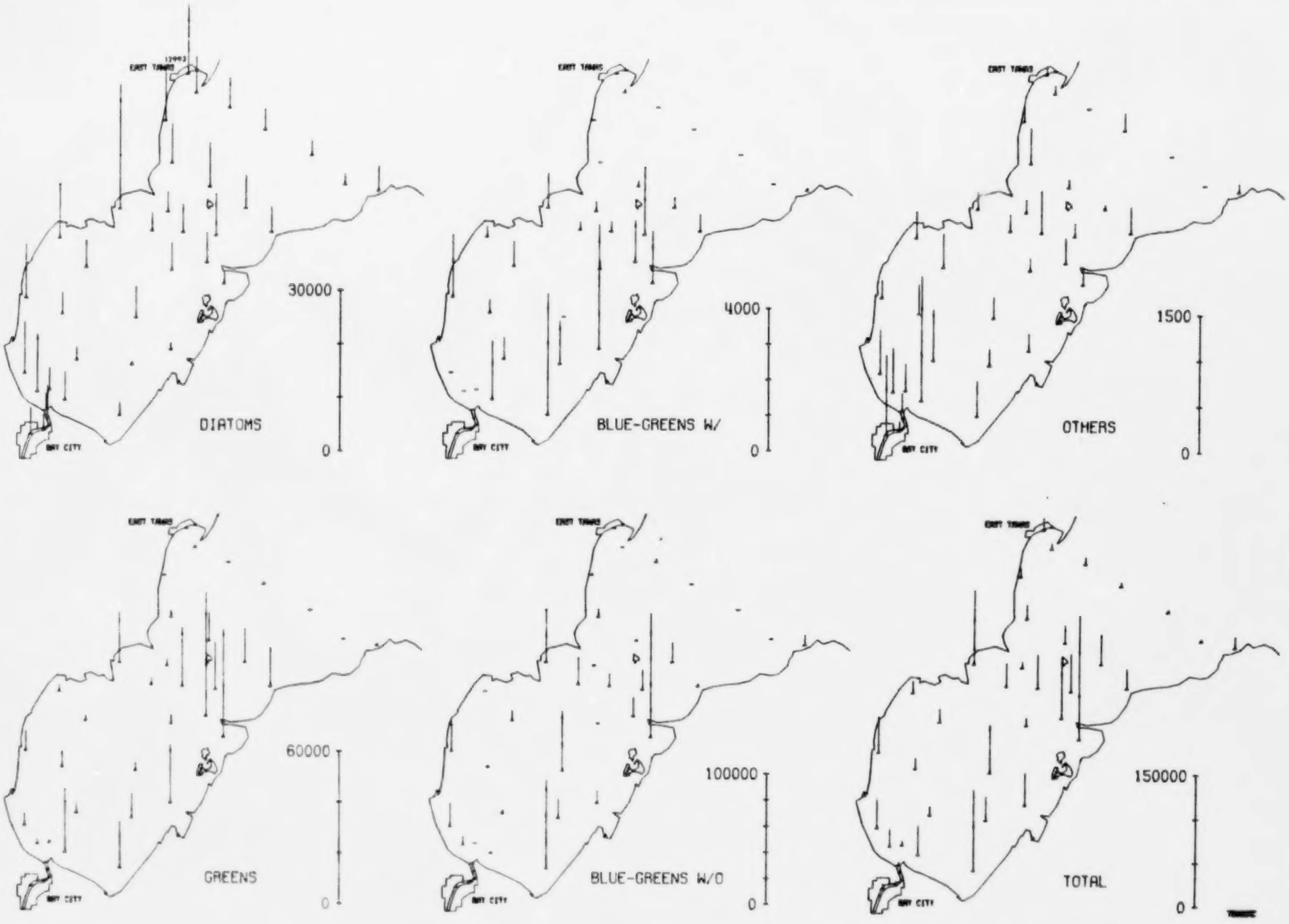
species common in the Lake Huron flora. Populations in the inner bay were mostly species which thrive under eutrophic conditions and the populations in the Saginaw River were taxa tolerant of extreme eutrophication and elevated salinity. As had been the case during the previous sampling, flagellates were a relatively minor constituent of the total phytoplankton assemblage and largest populations were found at stations near the mouth of the Saginaw River.

The next sampling was undertaken beginning 3 September (Fig. 23). Maximum total phytoplankton abundance again increased and the flora was dominated by extremely large concentrations of green and blue-green algae, particularly at a series of stations in the vicinity of Sand Point. The distribution of diatoms was essentially opposite that of the green and blue-green algae, with greatest abundance of this group occurring at stations along the northern coast of the bay. Some diatom populations were present at all stations sampled, but there again was a large qualitative difference in the diatom floras of different parts of the bay.

Only a very limited number of stations were sampled during the next cruise, which began 23 September (Fig. 24), due to adverse weather conditions. The stations sampled were all in the northern half of the bay, in segments 1, 2, and 4. Based on this subset, total phytoplankton abundance appeared to decline. Diatoms were most abundant, although significant populations of blue-green algae were present at stations in the inner bay. The abundance of green algae was much reduced and large populations were noted only at Station 30. Flagellates were a minor element of most assemblages sampled. They were most abundant at stations in the Saginaw River and, as was also the case with the diatoms, different populations were present in the river and lower bay than in the outer bay.

During the next sampling cruise, which began 9 October (Fig. 25), phytoplankton distribution in the bay was atypical, compared to other months sampled. Total phytoplankton abundance increased, and green algae were the dominant element of the flora at most stations sampled. Large populations were present in the Saginaw River and at shoreward stations along the southern coast and this group was atypically abundant at all stations sampled except for three stations in the Tawas Bay area. Blue-green algae were also relatively abundant in the lower bay and significant populations occurred even at the outermost line of stations sampled. During this sampling period the total abundance of diatoms was relatively uniform throughout the bay, but different species occupied different regions within the bay. Large populations of species usually associated with more oligotrophic or open lake conditions were noted in the Tawas Bay area.

During the next sampling period, which began 27 October (Fig. 26), several stations in segment 3, which usually have high levels of phytoplankton standing crop, were not sampled. The omission of these stations was particularly unfortunate in this case because the highest abundance of total phytoplankton was found at stations bordering the area which was not sampled, and it is quite likely that the highest levels of phytoplankton abundance in the entire bay actually occurred in the area represented by the missing stations. This supposition is supported, to a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BAY CITY
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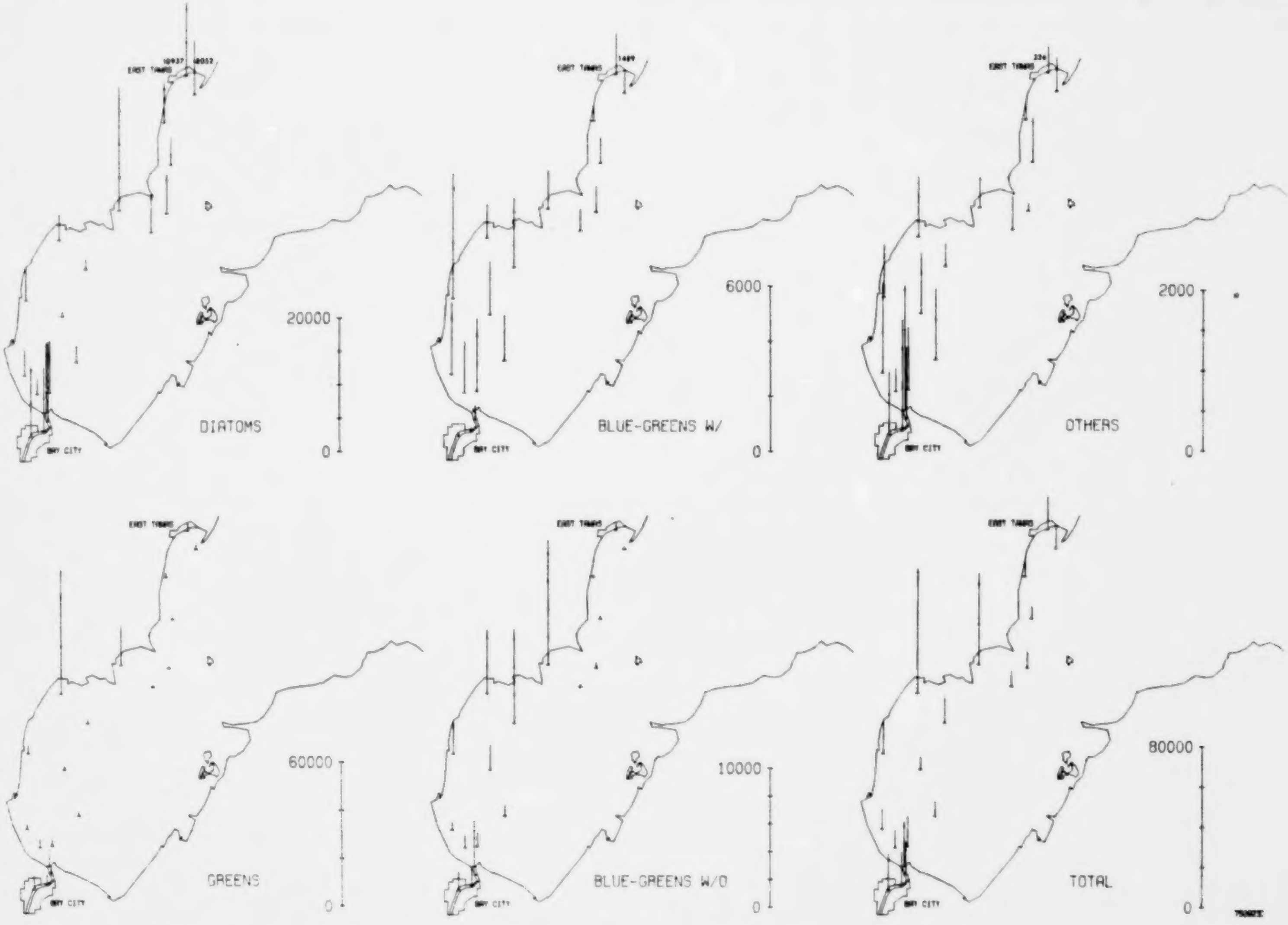
30000
0
BLUE-GREENS W/
4000
0
OTHERS
1500
0
GREENS
60000
0
BLUE-GREENS W/O
100000
0
TOTAL
150000
0

Figure 23. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 3 September 1975.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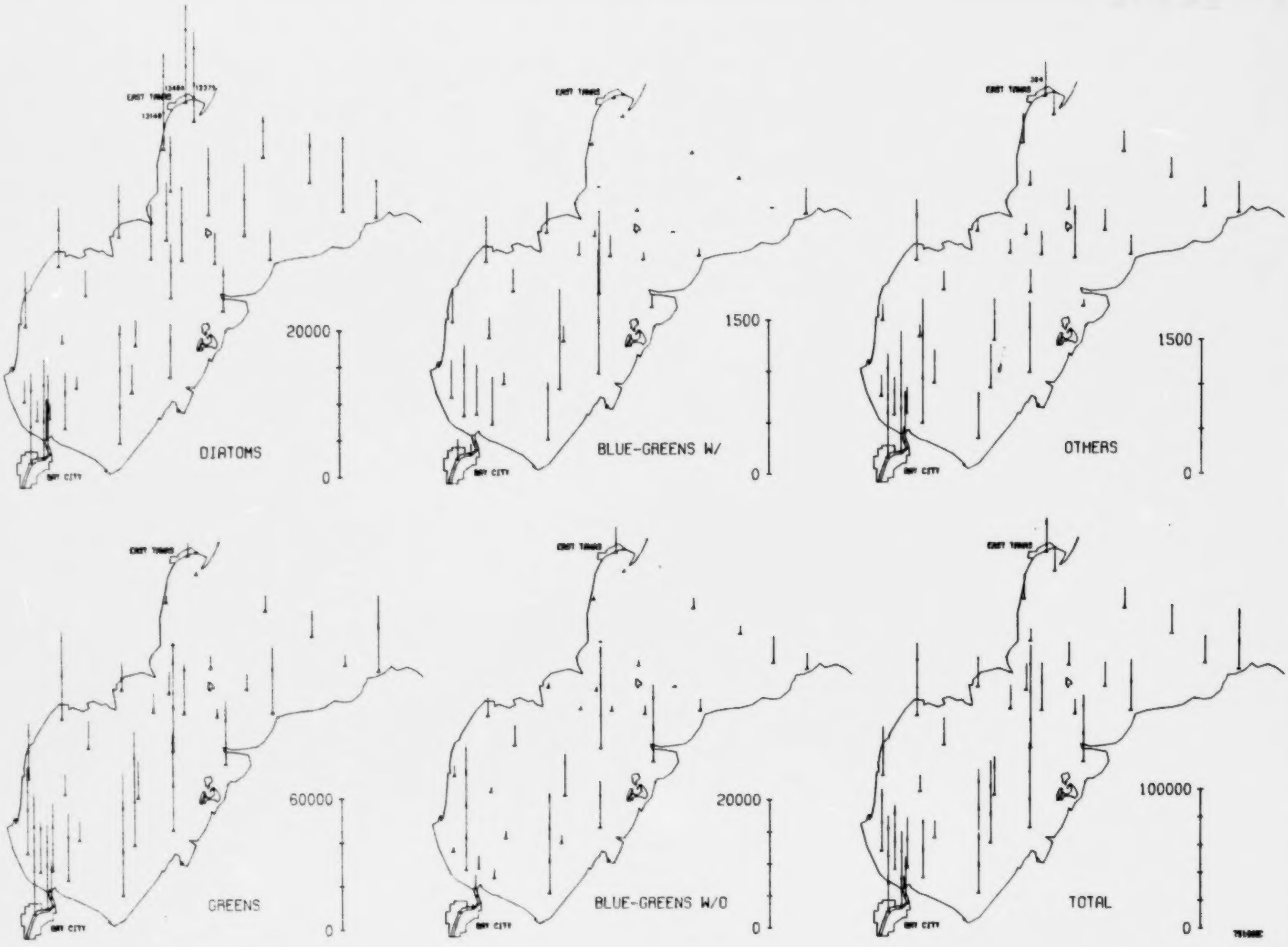
10052
BAY CITY
DIATOMS
20000
0
EAST TAWAS
1489
BAY CITY
BLUE-GREENS W/
6000
0
EAST TAWAS
234
BAY CITY
OTHERS
2000
0
EAST TAWAS
BAY CITY
GREENS
60000
0
EAST TAWAS
BAY CITY
BLUE-GREENS W/O
10000
0
EAST TAWAS
BAY CITY
TOTAL
80000
0

Figure 24. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 23 September 1975.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BAY CITY
DIATOMS
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BLUE-GREENS W/
1500
0
304
OTHERS
1500
0
GREENS
60000
0
BLUE-GREENS W/O
20000
0
TOTAL
100000
0

Figure 25. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 9 October 1975.

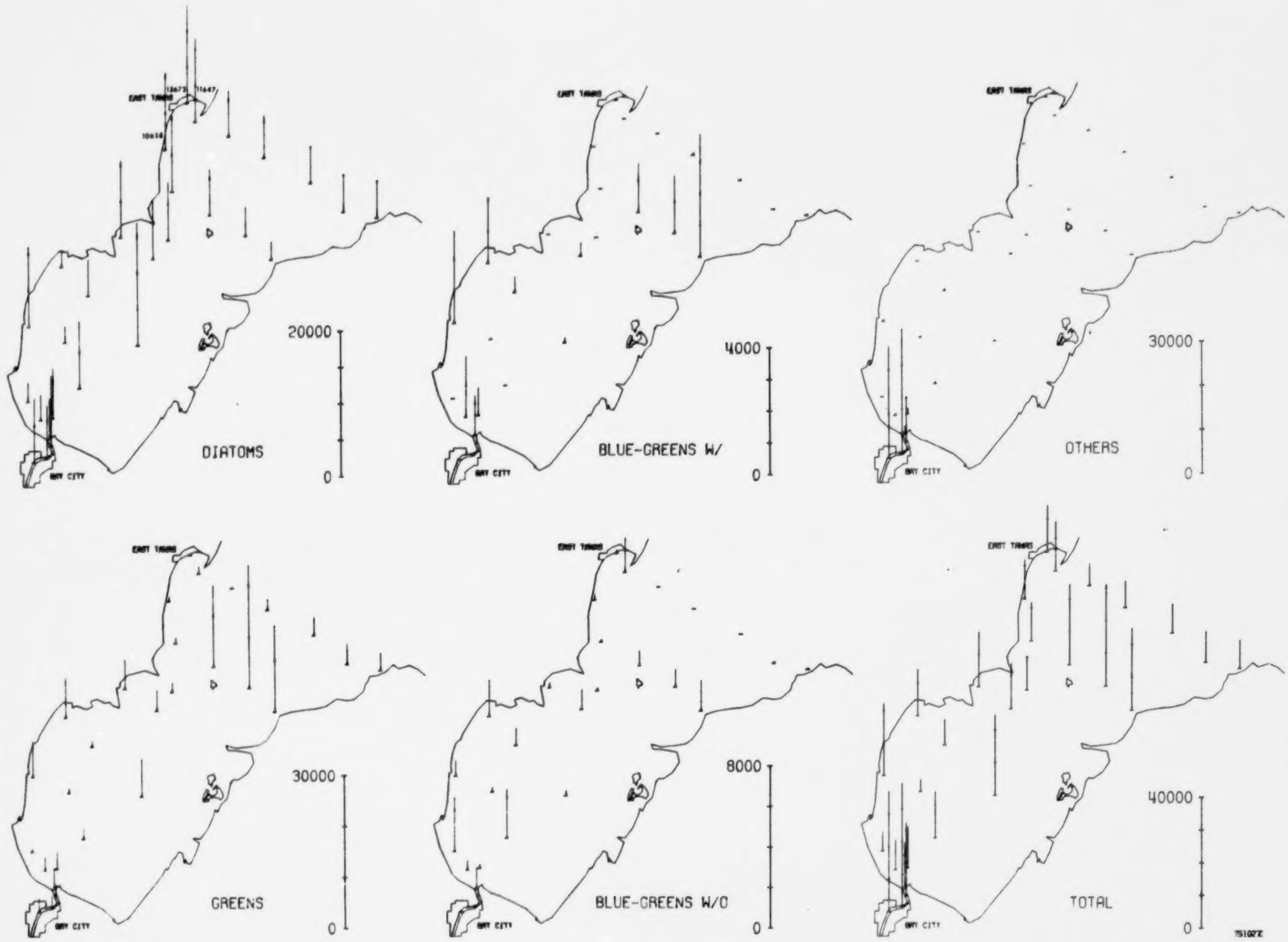

13672
11647
10658
EAST TAWAS
BAY CITY
DIATOMS
20000
0
BLUE-GREENS W/
4000
0
OTHERS
30000
0
GREENS
30000
0
BLUE-GREENS W/O
8000
0
TOTAL
40000
0
751027

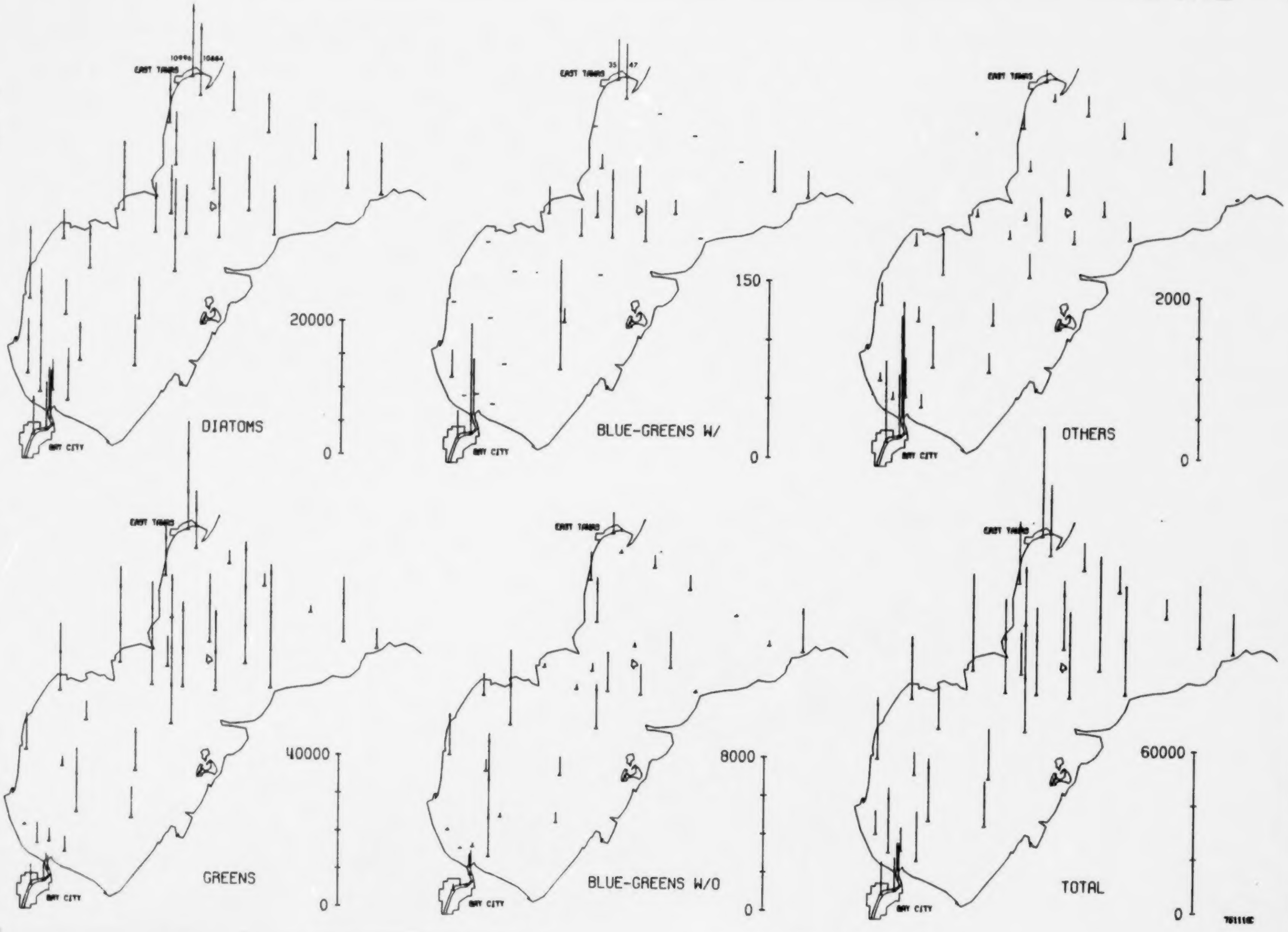
Figure 26. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 27 October 1975.

certain extent, by the distribution of the major phytoplankton groups. Green and blue-green algae are atypically abundant at Stations 42, 43, and 44, which may indicate that these populations are being generated in the unsampled area along the southern coast, as was the case in several previous cruises, and then transported to these stations. The trend in diatom abundance at these stations is opposite that of the heterocyst-forming blue-green algae. Diatoms are relatively evenly distributed at the stations sampled, compared to other groups of phytoplankton, but different species were present in the outer bay than in the inner bay. Conditions at Stations 42, 43, and 44 are apparently less conducive to the growth of diatom species occurring in the lower bay than to the green and blue-green algae. The distribution of flagellates during this sampling period is highly atypical. Large populations occur in the Saginaw River, but they are a minor component of phytoplankton assemblages in the rest of the bay.

More complete sampling was achieved during the next cruise, which began 16 November, although some stations along the southeastern shore of the bay were again omitted (Fig. 27). By this time, total phytoplankton abundance had increased somewhat at the stations sampled, and the abundance of phytoplankton was remarkably uniform throughout the bay. The distribution of major groups during this period was unusual. Green algae were unusually abundant at this time and very large populations were present at stations in the outer bay, including some stations in the Saginaw Bay-Lake Huron interface region. Relatively low abundance of this group was found at stations in the lower bay, particularly those in the immediate vicinity of the Saginaw River discharge. The trend in distribution of this group is thus essentially opposite that observed during most other cruises. The distribution of blue-green algae was somewhat similar, although the occurrence of representatives of this group were so scattered that any trend is somewhat obscured. The abundance of diatoms was again fairly uniform throughout the bay but different populations were characteristic of different areas of the bay. Flagellates remained abundant in the Saginaw River, but were relatively more abundant at other stations than they had been the previous month. As was the case with the diatoms, different species occurred in the river than in the rest of the bay, and there was further differentiation between stations in the inner bay and stations in the Lake Huron interface region.

The next sampling cruise began 16 December (Fig. 28). Due to adverse weather conditions only a limited number of stations were sampled, all in the inner bay. Total phytoplankton abundance at the stations sampled was drastically reduced from levels observed the previous month. Diatoms were the dominant element of the flora, although significant populations of green and blue-green algae were found at some stations. Not enough stations were sampled to establish regional trends.

A similar limited array of stations was sampled during the next cruise, which began 27 January 1976 (Fig. 29). Total phytoplankton abundance was further reduced, but there was a trend for highest total phytoplankton abundance to occur at stations in segment 3. The main group contributing to this pattern was the green algae which were the dominant element of the flora during this period. Blue-green algae without heterocysts and flagellates had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10884
BAY CITY
DIATOMS
20000
0
EAST TAWAS
35
47
BAY CITY
BLUE-GREENS W/
150
0
EAST TAWAS
BAY CITY
OTHERS
2000
0
EAST TAWAS
BAY CITY
GREENS
40000
0
EAST TAWAS
BAY CITY
BLUE-GREENS W/O
8000
0
EAST TAWAS
BAY CITY
TOTAL
60000
0
751116C

Figure 27. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 16 November 1975.

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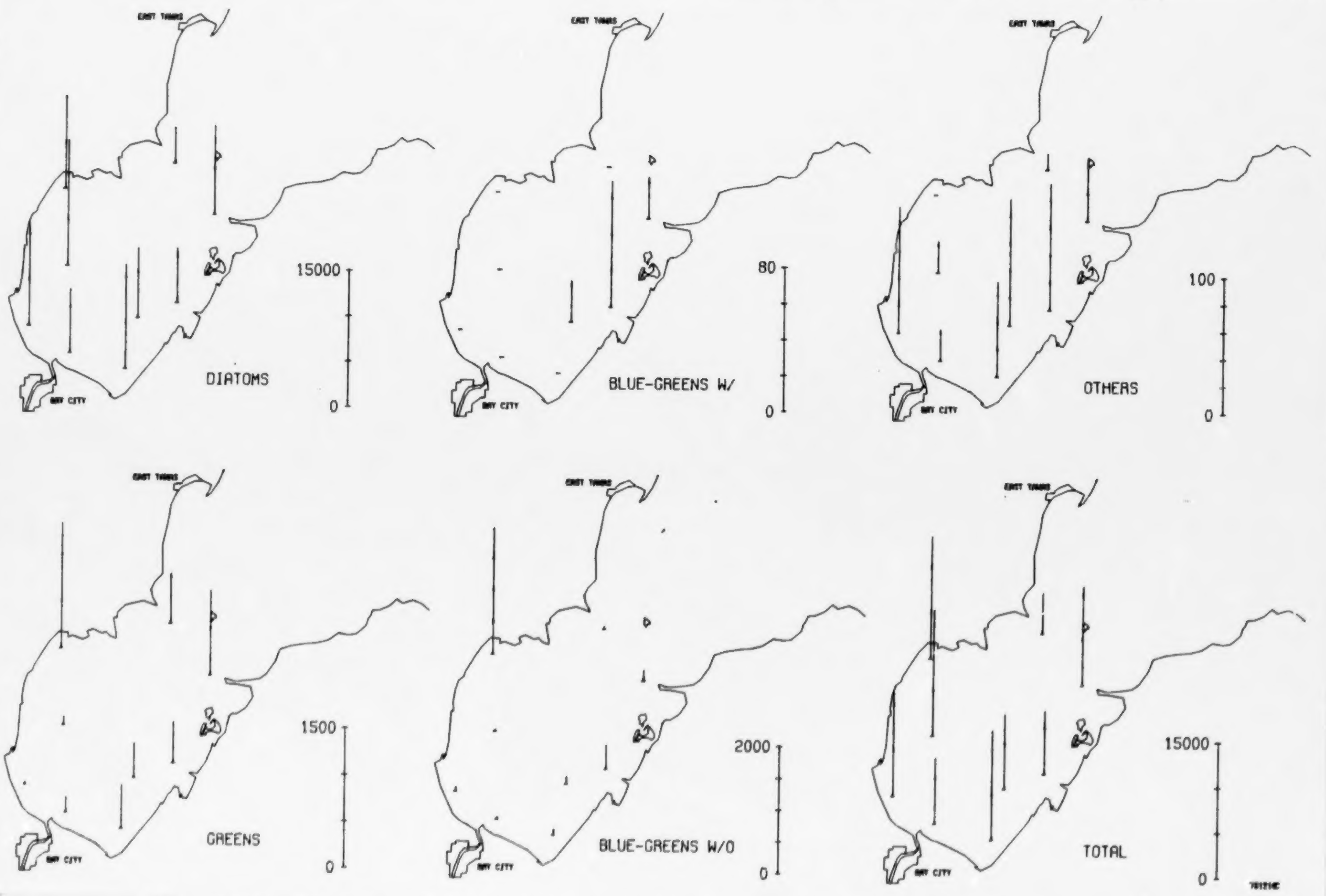
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BAY CITY
DIATOMS
15000
0
BLUE-GREENS W/
80
0
OTHERS
100
0
GREENS
1500
0
BLUE-GREENS W/O
2000
0
TOTAL
15000
0

Figure 28. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 16 December 1975.

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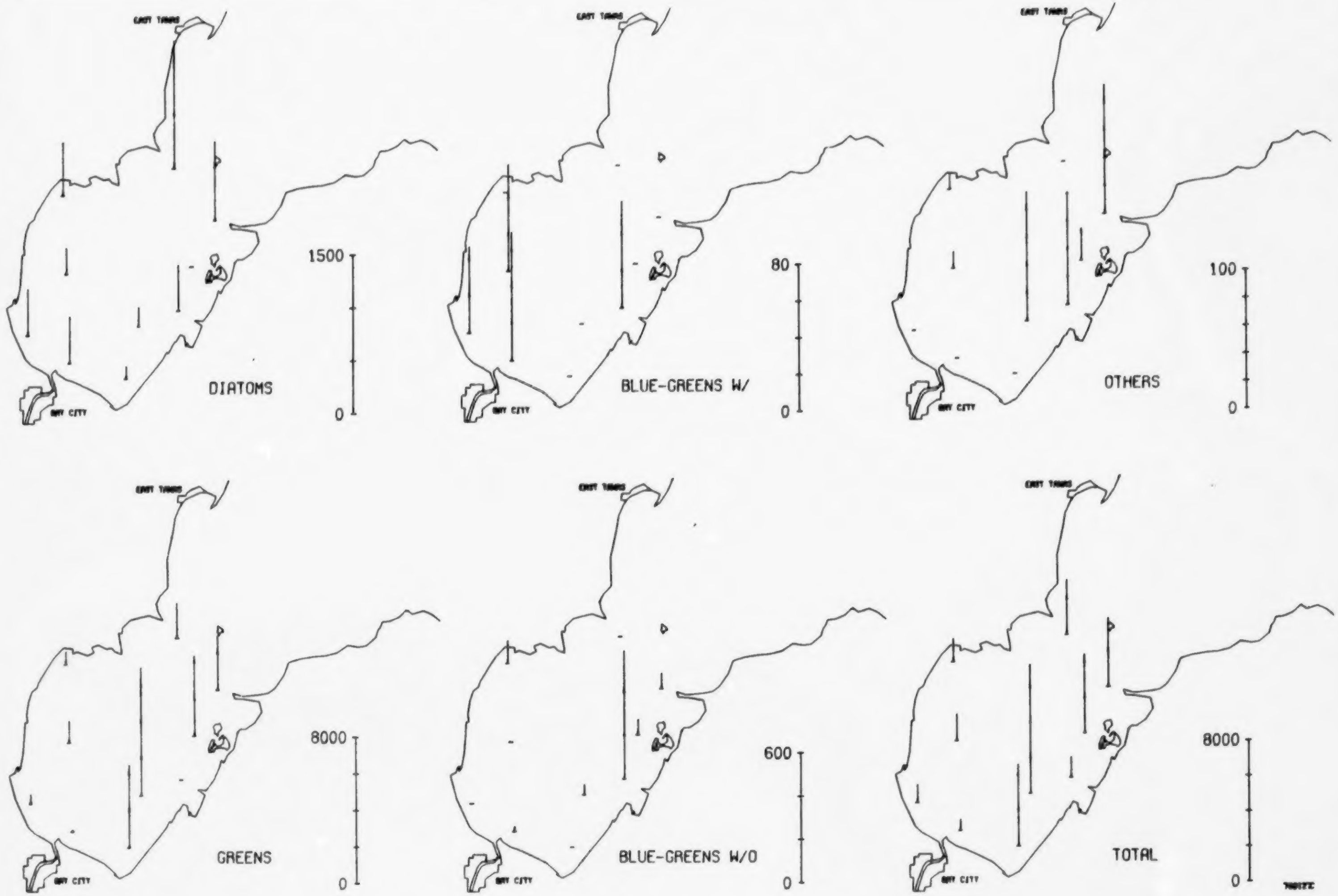
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BAY CITY
DIATOMS
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0
BLUE-GREENS W/
80
0
OTHERS
100
0
GREENS
8000
0
BLUE-GREENS W/O
600
0
TOTAL
8000
0

Figure 29. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 27 January 1976.

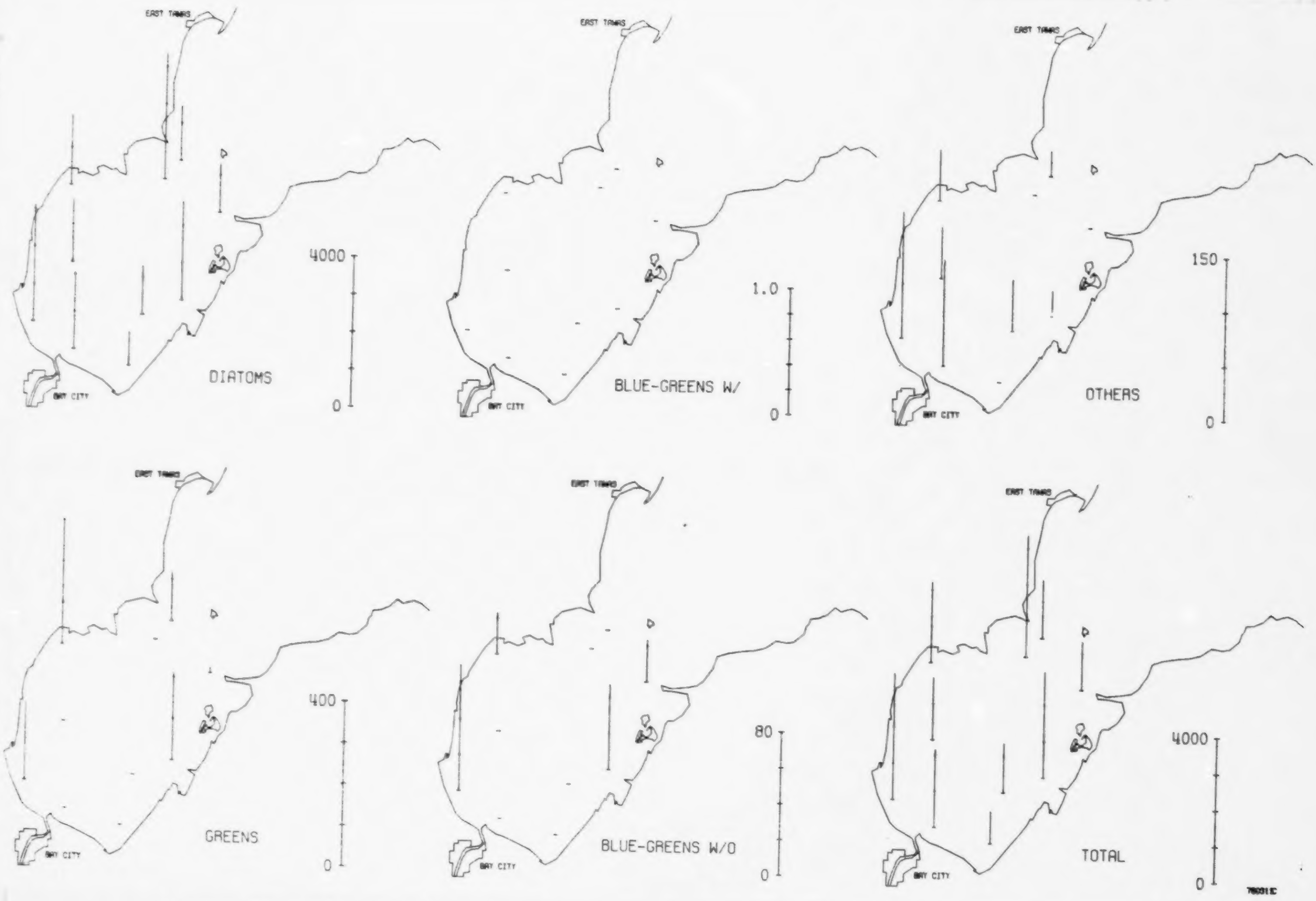
similar distribution patterns to the green algae, although they were minor components of the flora at this time. Heterocyst-forming blue-green algae were very rare. Diatoms were the second most abundant of the major groups and the trend in abundance of this group was opposite the others.

Seasonal low in total phytoplankton abundance was found on the next cruise, which began 11 March 1976 (Fig. 30). The abundance of total phytoplankton was low at all stations sampled and abundance was fairly uniform. The same series of stations was sampled as in the previous month. Only scattered populations of green and blue-green algae were noted, with most occurrences at nearshore stations. Heterocyst-forming blue-green algae were not noted in any of the samples from this cruise.

During the next cruise, which began 27 April (Fig. 31), and in subsequent cruises in the sequence, the array of stations sampled in the project was reduced. Fewer stations were sampled in the lower bay and intermediate lines of stations in the outer bay were eliminated. This reduction in station density, and particularly the elimination of stations in the transitional zone between the lower bay and the Lake Huron interface, considerably reduced resolution in detecting trends in phytoplankton abundance. During the 27 April cruise total phytoplankton abundance increased with highest total abundance occurring at stations in mid-bay. The flora was dominated by diatoms but green algae were an important element of assemblages at several stations in the lower bay. Flagellates were widely distributed, but their abundance was less than diatoms or green algae and, as had been the case in several previous cruises, the trend in abundance of flagellates tended to be opposite the trend in abundance of diatoms at stations in the lower bay. At stations in the Lake Huron interface region the abundance trends of these two groups were similar.

There was a very striking difference in the abundance and species composition of phytoplankton assemblages collected at stations in the Lake Huron interface region versus other stations sampled in the bay during the next cruise, which began 12 May (Fig. 32). The apparent difference was enhanced by the fact that the intermediate line of stations was not sampled, as it had been in previous years. The differences in abundance and species composition were, however, larger than had been observed in previous spring sampling periods. Diatoms were the dominant element of the flora at most stations sampled, although green algae were very abundant at a few mid-bay stations. Highest numbers of flagellates and blue-green algae were found at a line of stations southwest of Charity Island. Although the flagellate groups were considerably more abundant than blue-greens, the similarity in distribution was striking.

Only a limited number of stations were sampled on the next cruise, which began 1 June (Fig. 33), due to adverse weather conditions. All of the stations sampled were in the lower bay. Total phytoplankton abundance increased at these stations, and extremely dense populations of green algae were noted at stations in the vicinity of the Saginaw River mouth. Diatoms remained relatively abundant as did flagellates, and atypically large populations of flagellates were found at stations in the Saginaw River. Blue-green algae were a fairly minor component of the flora and their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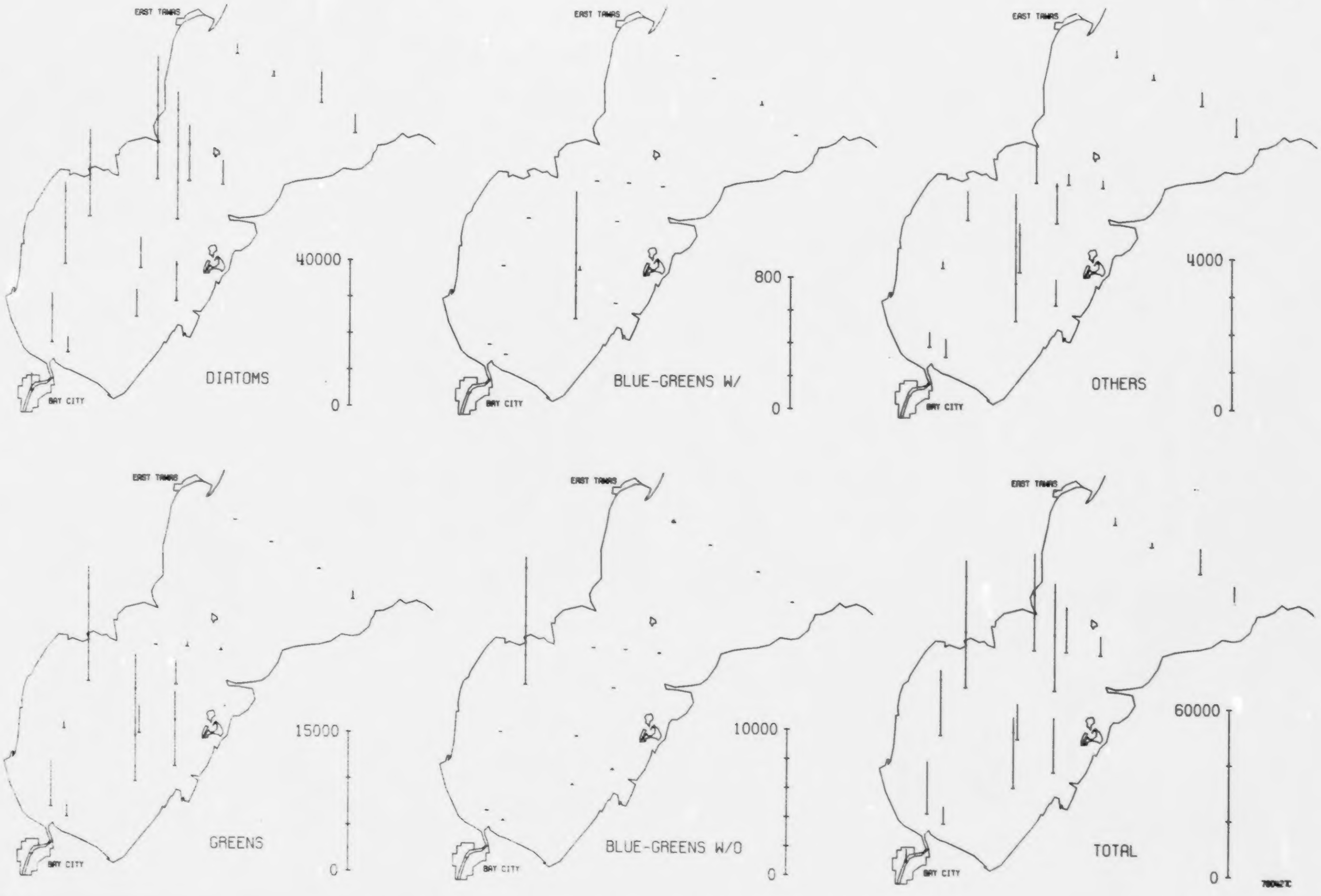
BAY CITY
DIATOMS
4000
0
BLUE-GREENS W/
1.0
0
OTHERS
150
0
GREENS
400
0
BLUE-GREENS W/O
80
0
TOTAL
4000
0
78031E

Figure 30. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 11 March 1976.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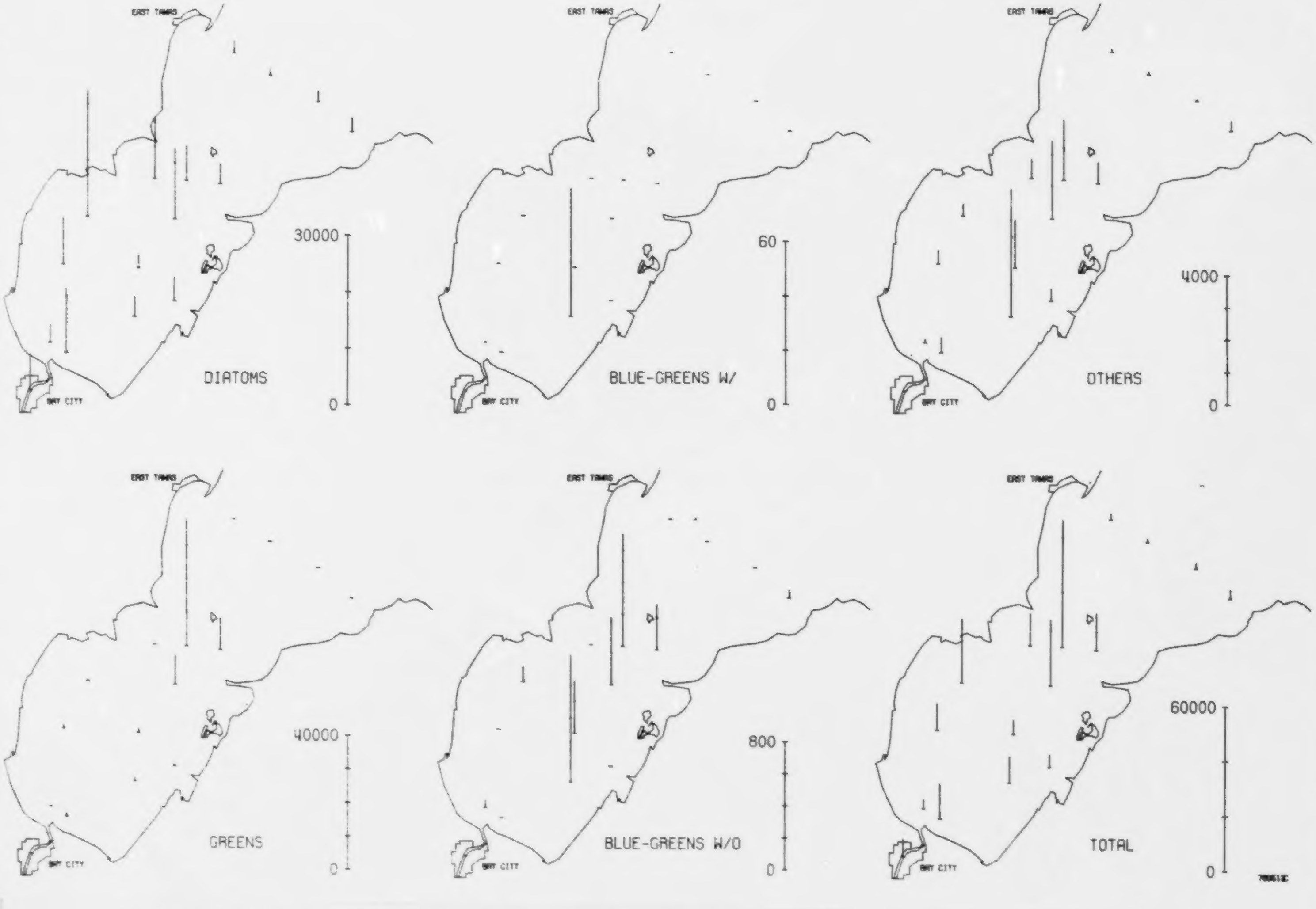
BAY CITY
DIATOMS
40000
0
BLUE-GREENS W/
800
0
OTHERS
4000
0
GREENS
15000
0
BLUE-GREENS W/O
10000
0
TOTAL
60000
0
760427C

Figure 31. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 27 April 1976.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BAY CITY
DIATOMS
30000
0
BLUE-GREENS W/
60
0
OTHERS
4000
0
GREENS
40000
0
BLUE-GREENS W/O
800
0
TOTAL
60000
0
780613C

Figure 32. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 12 May 1976.

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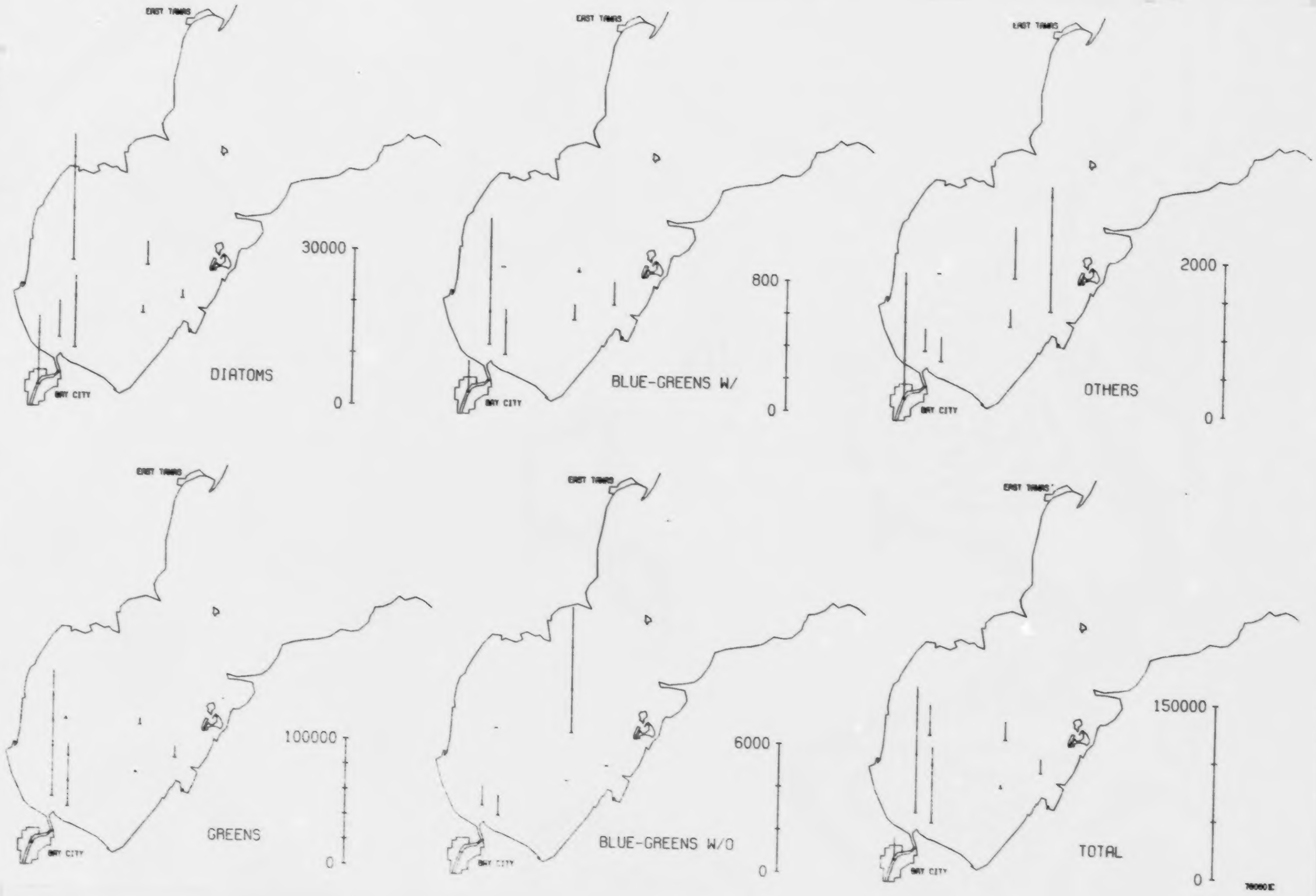
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BAY CITY
DIATOMS
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0
BLUE-GREENS W/
800
0
OTHERS
2000
0
GREENS
100000
0
BLUE-GREENS W/O
6000
0
TOTAL
150000
0

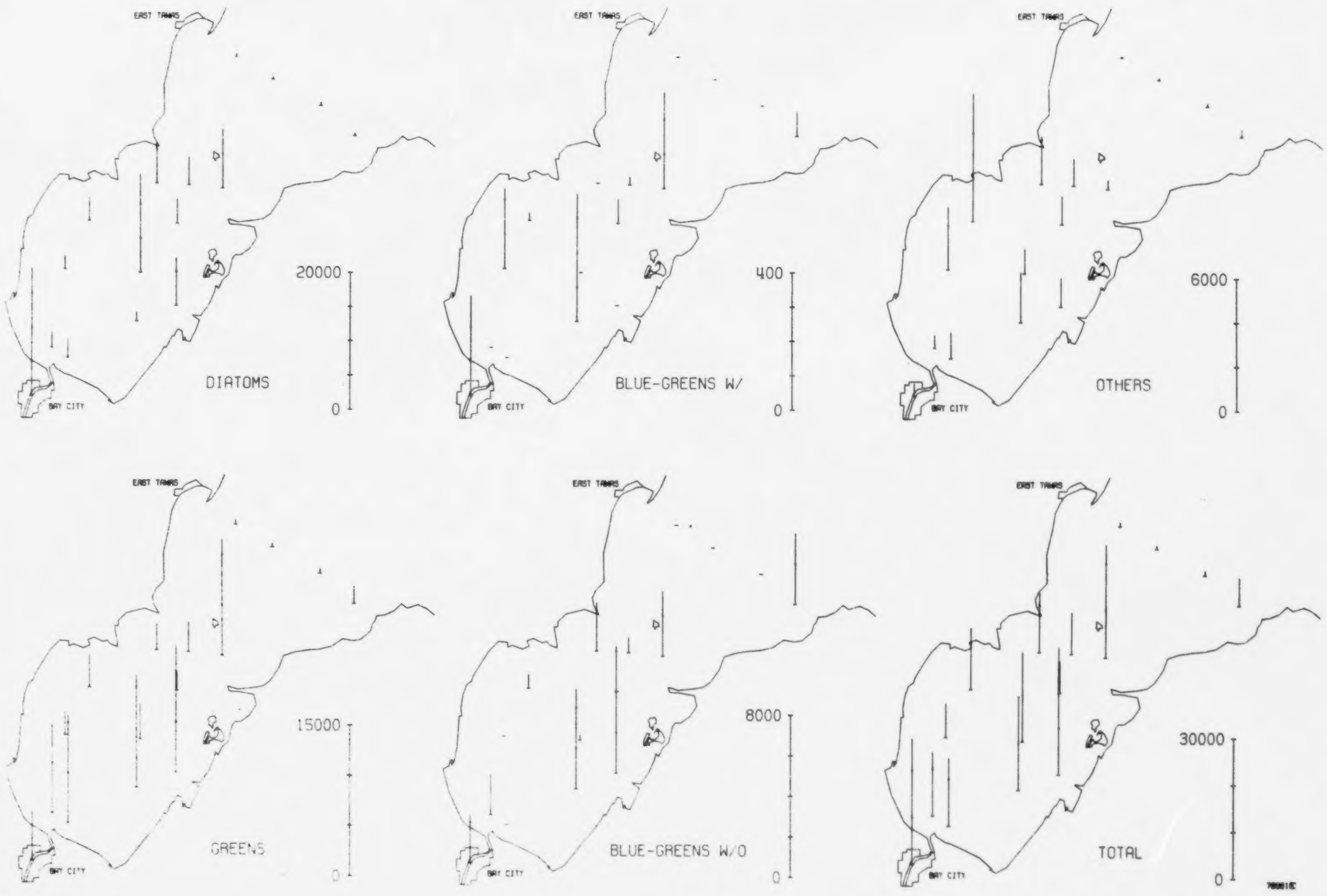
Figure 33. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 1 June 1976.

distribution was scattered. Highest numbers of heterocyst-forming blue-greens were found at stations near the Saginaw River mouth which had highest total phytoplankton abundance and highest abundance of green algae.

More complete sampling was obtained on the next cruise, which began 18 June (Fig. 34). Maximum total phytoplankton abundance was reduced from the extreme levels noted the previous month. Diatoms remained an important element of assemblages at most stations sampled, although their abundance relative to other groups was reduced. Highest numbers of diatoms were found at a station in the Saginaw River. As had been the case in most previous sampling periods, the species composition of the river station was substantially different from stations in the bay. Green algae, flagellates, and blue-green algae all increased in importance. Greens and blue-greens tended to be most abundant at stations along the southern coast of the bay while the flagellate groups tended to be most abundant at stations in the northern sector of the lower bay. During this sampling period many populations of green and blue-green algae characteristic of eutrophic water and generally abundant at stations in lower Saginaw Bay were found at the most southerly station in the Lake Huron interface. It appeared that these populations were being advected out of the bay along the southern shore as had been the case in several other summer cruises.

During the next cruise, which began 8 July (Fig. 35), much higher total phytoplankton abundance was observed, particularly at stations in the lower bay. Blue-green algae were the dominant component of the flora in the lower bay. Heterocyst-forming species were a relatively minor fraction of the total blue-green algae observed, but they were fairly abundant at Stations 13, 24, and 33. Green algae were also very abundant in the lower bay. Numbers of diatoms reduced at most stations sampled but large populations were present in the Saginaw River and at Station 13 near the mouth of the river. The species present at these stations were mostly small centrics tolerant of high conservative ion levels and extremely eutrophic conditions. During this sampling period there was little evidence of dispersal of populations generated in the lower bay into Lake Huron. Green algal abundance was higher at Station 52 than at other stations in the Lake Huron interface, but other groups did not show this distribution pattern.

During the next cruise, which began 28 July (Fig. 36), the same general pattern of distribution was observed. Total phytoplankton abundance continued to increase in the lower bay, and there was an extreme difference in both abundance and species composition between stations in the lower bay and stations in the Lake Huron interface region. Blue-green algae continued to be the dominant element of assemblages at stations in the lower bay, particularly at stations in the southeastern quadrants. Green algae increased in relative and absolute abundance and the distribution pattern of this group was similar to that of the blue-green algae. The abundance of diatoms and flagellates increased somwhat at stations in the open bay from levels observed during the previous sampling period. The abundance patterns for these groups were opposite those of the green and blue-green algae. As had been the case previously, diatom abundance was highest in the Saginaw River, but the species composition at this station was strikingly different from that found at stations in the open waters of the bay. Populations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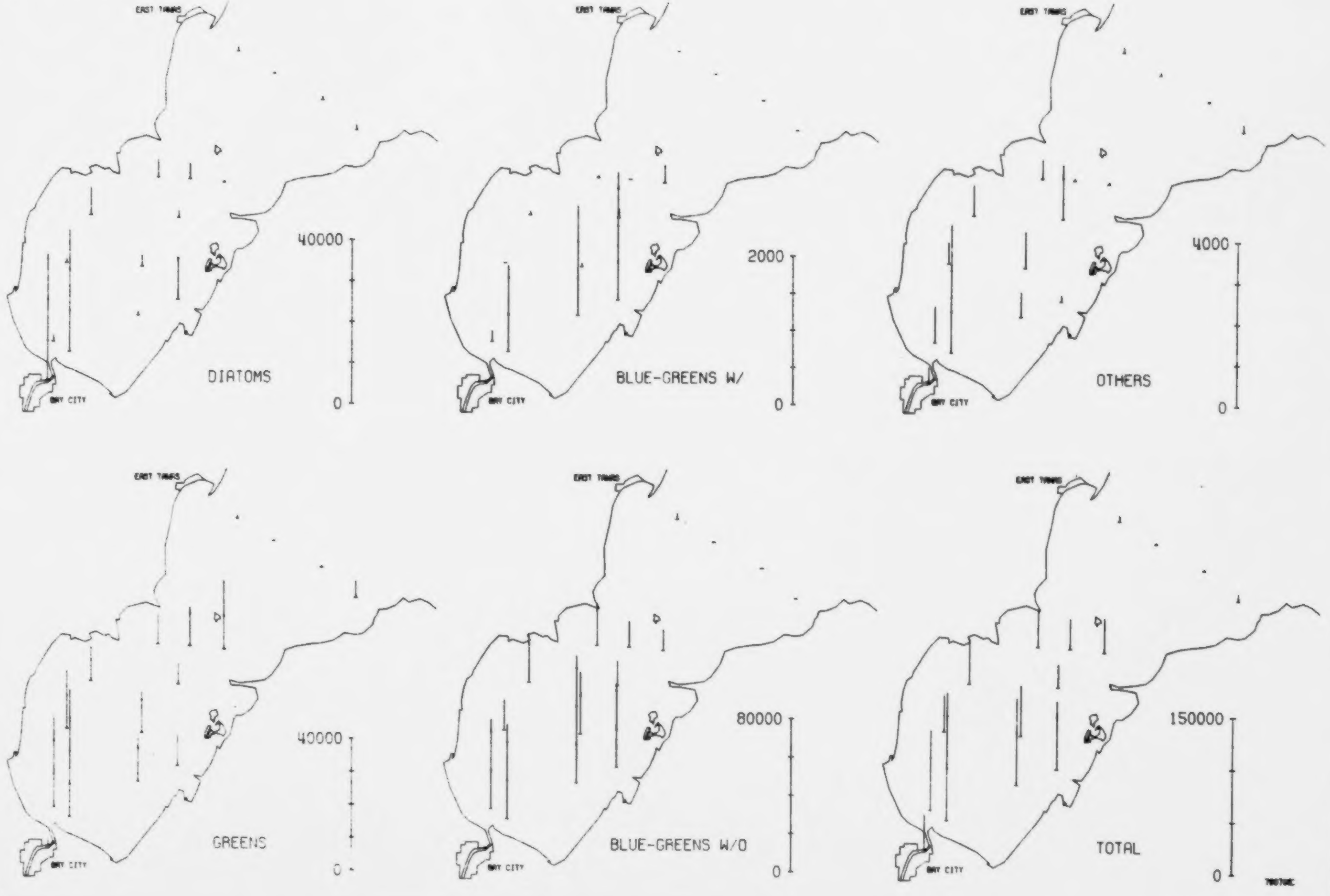
DIATOMS
20000
0
BLUE-GREENS W/
400
0
OTHERS
6000
0
GREENS
15000
0
BLUE-GREENS W/O
8000
0
TOTAL
30000
0

Figure 34. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 18 June 1976.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BAY CITY
DIATOMS
40000
0
BLUE-GREENS W/
2000
0
OTHERS
4000
0
GREENS
40000
0
BLUE-GREENS W/O
80000
0
TOTAL
150000
0

Figure 35. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 8 July 1976.

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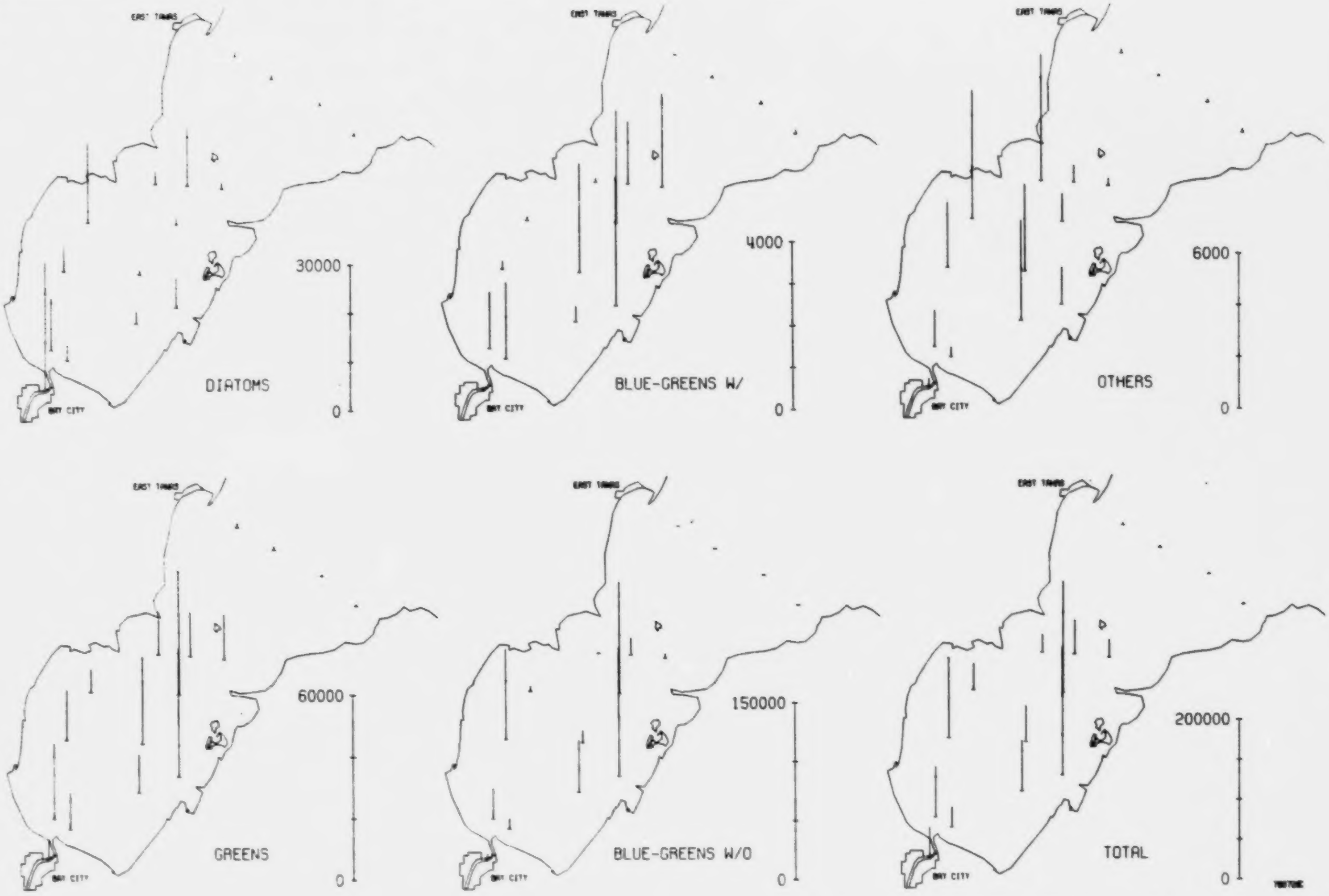
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BAY CITY
DIATOMS
30000
0
BLUE-GREENS W/
4000
0
OTHERS
6000
0
GREENS
60000
0
BLUE-GREENS W/O
150000
0
TOTAL
200000
0

Figure 36. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 28 July 1976.

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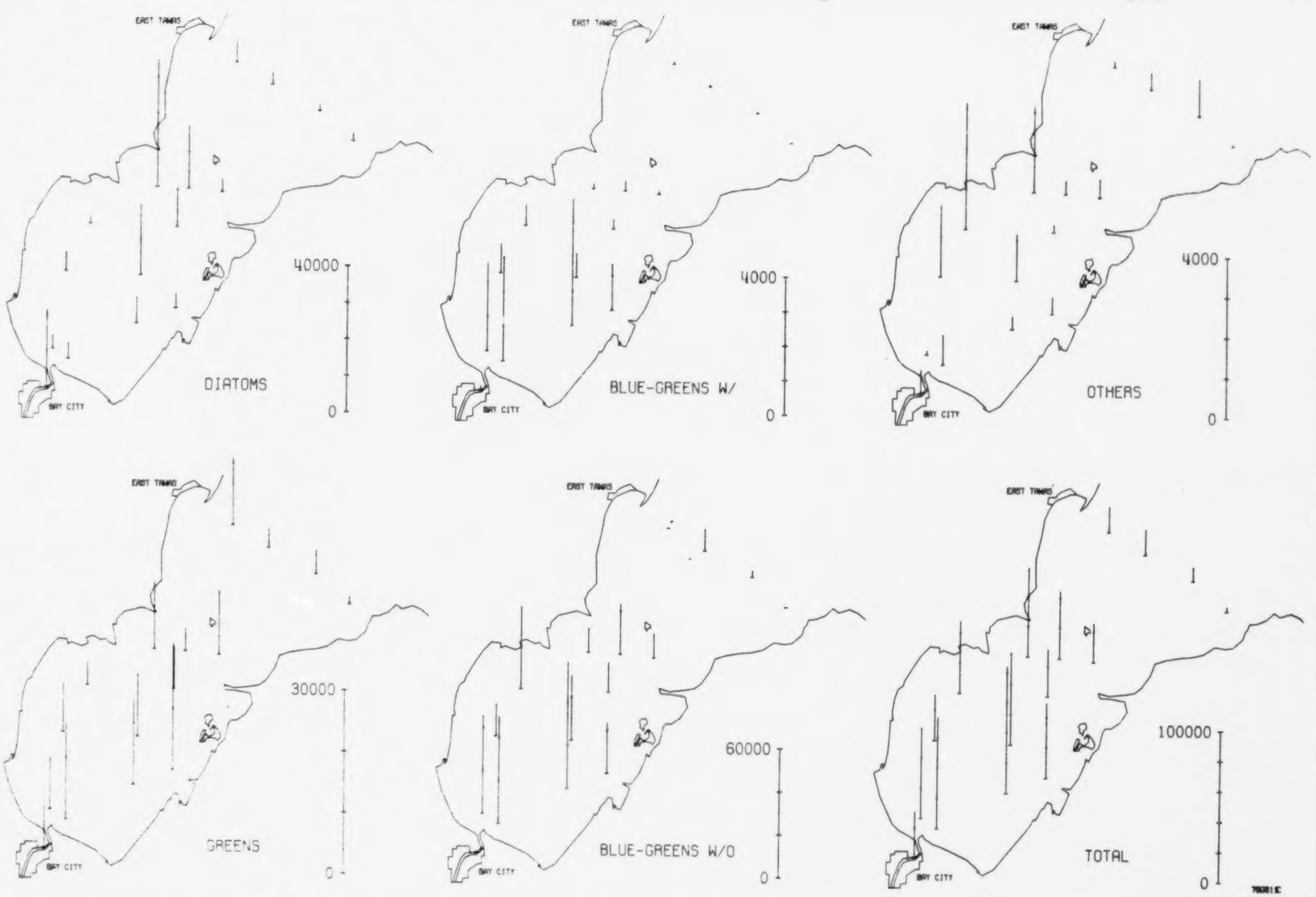
present at stations in the Lake Huron interface region were different from those found at stations in the lower bay.

This situation had changed somewhat by the time the next sampling cruise was undertaken, beginning 11 August (Fig. 37). Average total abundance of phytoplankton declined, but there was a marked increase in abundance at stations in the Lake Huron interface region. Unlike previous cruises, highest total phytoplankton abundance was found at stations on the northern end of the outer transect. Assemblages in the lower bay continued to be dominated by blue-green and green algae, but the abundance of diatoms increased, particularly at stations in the central segment of the bay. There was more similarity in assemblage composition between stations in the lower bay and those in the Lake Huron interface region than was the case in most cruises. Heterocyst-forming blue-green algae were much more abundant at stations in the lower bay, but small populations of the same species were found at stations in the Lake Huron interface. The same situation was typical of other groups as well. The diatom and green algal flora of the Saginaw River remained distinct, but there was an unusual degree of similarity in species composition at all other stations sampled. Although the same suite of species was present, abundance of the flagellate groups tended to run counter to the trend of the other major groups. The inverse relationship between the abundance of green algae and flagellates was particularly notable.

A somewhat more typical pattern was observed during the next sampling period, which began 31 August (Fig. 38). Total phytoplankton abundance increased at stations in the lower bay, but decreased slightly at stations in the Lake Huron interface region. Although there was some overlap of populations between the two regions, differences were much greater than they had been earlier in the month. Blue-green algae continued to dominate the flora at stations in the lower bay, and green algae were an important component of assemblages sampled in this region. Limited numbers of greens and blue-greens were found in samples from the outer line of stations, and highest abundance was noted at the northernmost and southernmost shoreward stations on this transect. Although this type of pattern might be expected to occur routinely, this was one of the few instances in which it was observed during the period in which we sampled the bay. The abundance of diatoms generally decreased, but their total abundance was more uniform than it was during the previous sampling period. Distinct suites of populations were again present at stations in the Saginaw River, the lower bay, and the Lake Huron interface region. Flagellates were most abundant at stations on the north side of the bay and the general pattern of abundance of this group tended to be opposite the abundance pattern of diatoms.

The next cruise in the sequence began 18 September (Fig. 39). Total phytoplankton abundance was reduced slightly, although high numbers were present at most stations in the lower bay. The flora of the lower bay continued to be dominated by blue-green and green algae. The abundance of diatoms was remarkably uniform throughout the bay, but very high numbers were present at the station sampled in the Saginaw River. Although numbers were similar, the species composition of assemblages in the river, the lower bay, and the Lake Huron interface region was greatly different. During this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BAY CITY
DIATOMS
40000
0
BLUE-GREENS W/
4000
0
OTHERS
4000
0
GREENS
30000
0
BLUE-GREENS W/O
60000
0
TOTAL
100000
0
78081E

Figure 37. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 11 August 1976.

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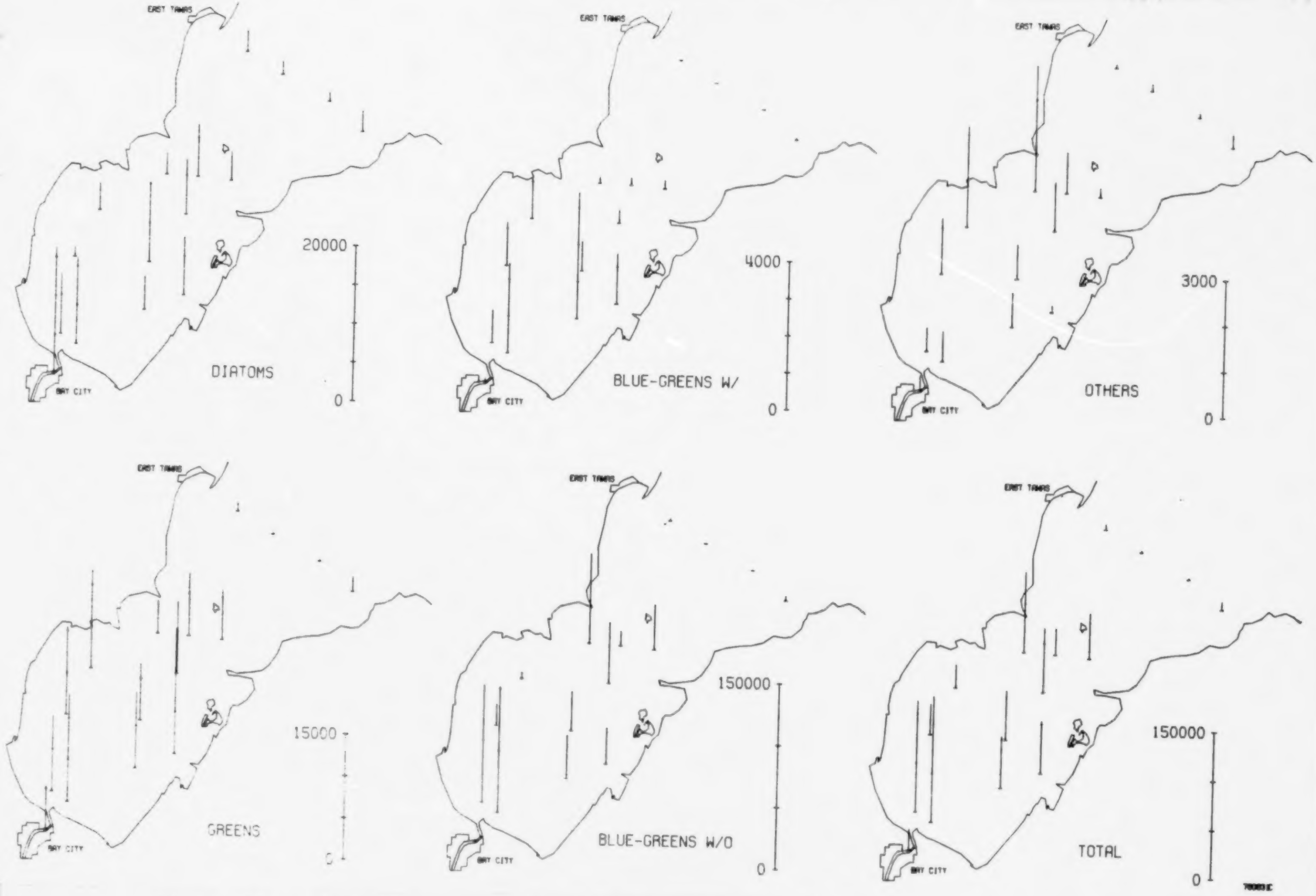
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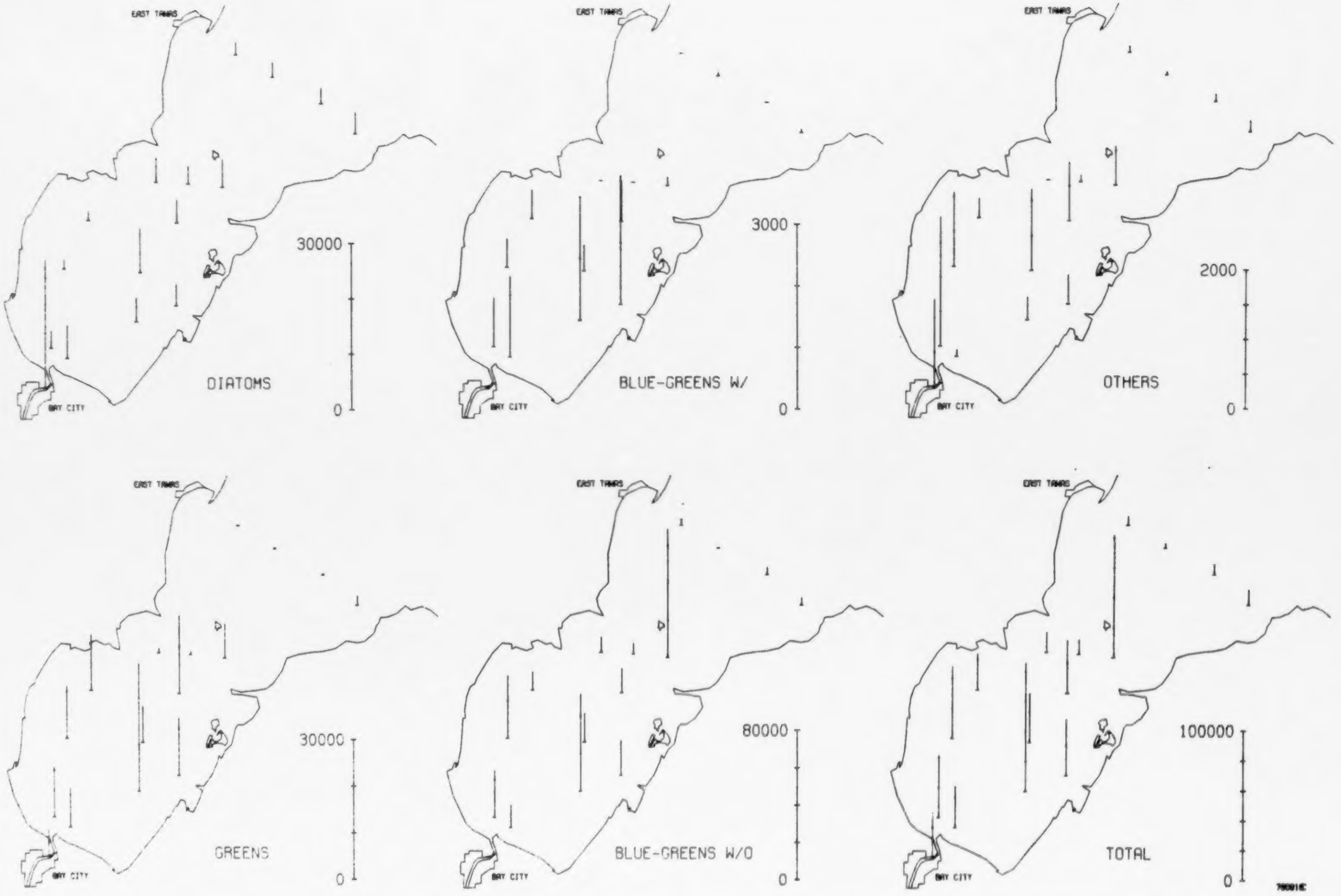
BAY CITY
DIATOMS
20000
0
BLUE-GREENS W/
4000
0
OTHERS
3000
0
GREENS
15000
0
BLUE-GREENS W/O
150000
0
TOTAL
150000
0

Figure 38. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 31 August 1976.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BAY CITY
DIATOMS
30000
0
BLUE-GREENS W/
3000
0
OTHERS
2000
0
GREENS
30000
0
BLUE-GREENS W/O
80000
0
TOTAL
100000
0

Figure 39. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 18 September 1976.

sampling period the abundance trends in the flagellate groups were similar to those of the green and blue-green algae but the difference in species composition in different regions was similar to that found in the diatoms.

Although some stations were omitted from the next sampling round, which began 7 October (Fig. 40), a reasonable coverage of the bay was obtained. On the basis of these samples, phytoplankton distribution within the bay was substantially similar to the case observed the previous month. Total phytoplankton abundance was slightly reduced, but very high total abundance was noted at several stations in the inner bay. Blue-green and green algae continued to dominate the flora, although population distribution was even more erratic than had been the case previously. Diatoms were again most abundant in the Saginaw River, with relatively uniform numbers throughout the open waters of the bay. The marked distinction in the species composition of assemblages found in the river, the lower bay, and the Lake Huron interface stations was maintained. A larger proportion of species tolerant of hypereutrophic conditions, which were usually found at stations in the inner bay, occurred at Stations 51 and 52 on the southeastern end of the outer transect of stations. These stations also contained a higher proportion of blue-green and green algae than the other stations on this transect, which is probably indicative of transport of water masses derived from the lower bay along the southern shore.

The final cruise in the project began 10 November (Fig. 41). Due to weather conditions at this time of year, a limited number of stations were sampled, mostly in the inner bay. Total phytoplankton abundance declined slightly at the stations sampled, and the distribution of major phytoplankton groups in the inner bay was quite unusual. Extreme abundance of green algae was noted at Station 56, north of Fish Point. Although representatives of this group were present at the other stations sampled, population densities did not approach those found at Station 56. The next highest abundance of green algae was found at stations near the mouth of the Saginaw River. Similar species were present at these stations and it is possible that the very high abundance of green algae at Station 56 is related to the output of the Saginaw River. Blue-green algae, on the other hand, were much more abundant at stations in the northern sector of the lower bay. Blue-green populations consisted of mostly non-heterocyst-forming species, although relatively low levels of species with heterocysts were found at stations in the inner bay. During this sampling period the distribution of diatoms ran counter to the trend observed for the blue-green algae. The highest population levels observed were found in the Saginaw River, but nearly equal population densities were found at stations in the inner bay. The highest abundance of diatoms occurred at stations in the southern sector of the lower bay. During this sampling period flagellates were present in minimal abundance and total abundance of the group was quite similar at all stations in the inner bay.

DISCUSSION

Taken in its entirety, the phytoplankton flora of Saginaw Bay is extremely diverse (Appendix 1). The species encountered in the bay span the

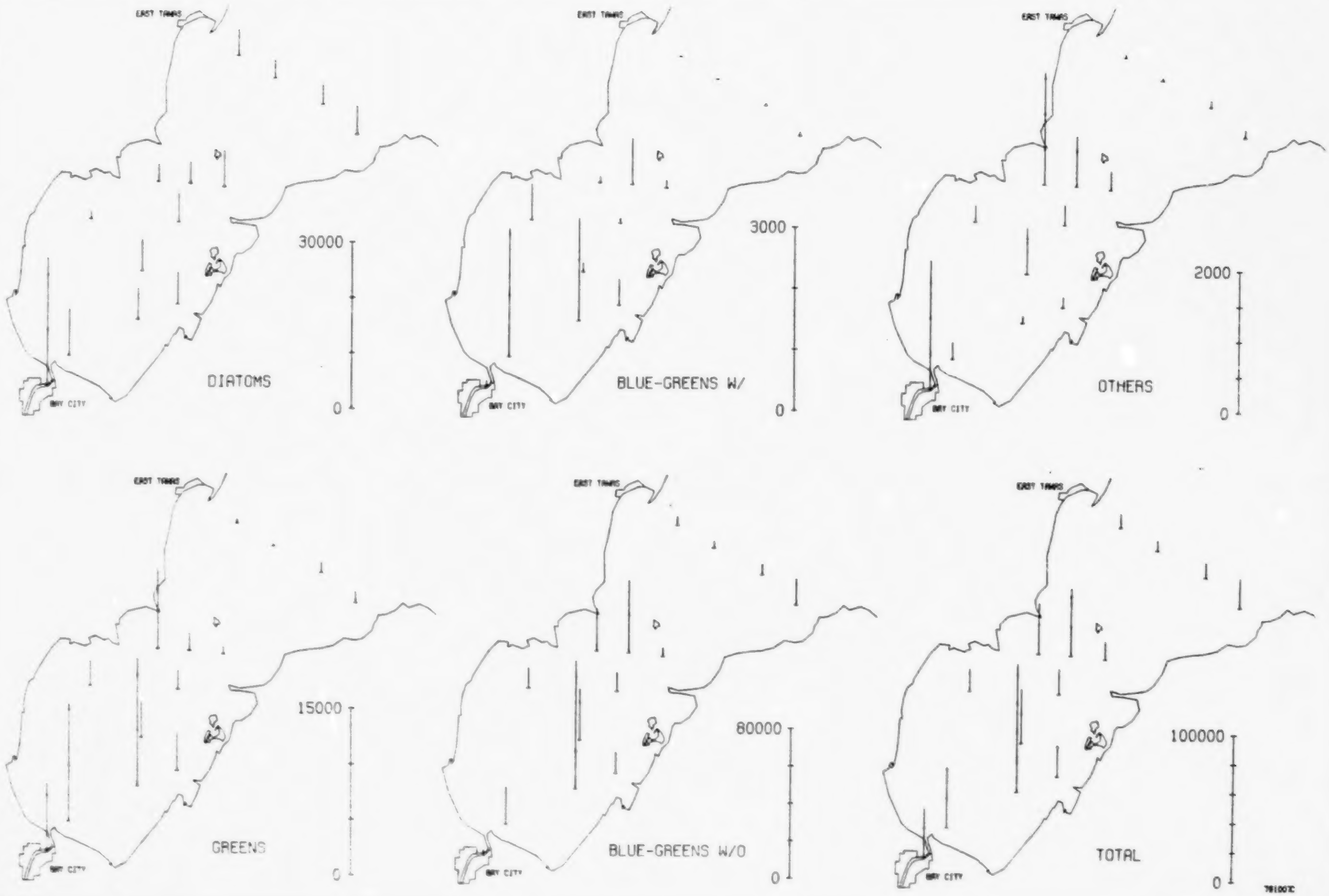
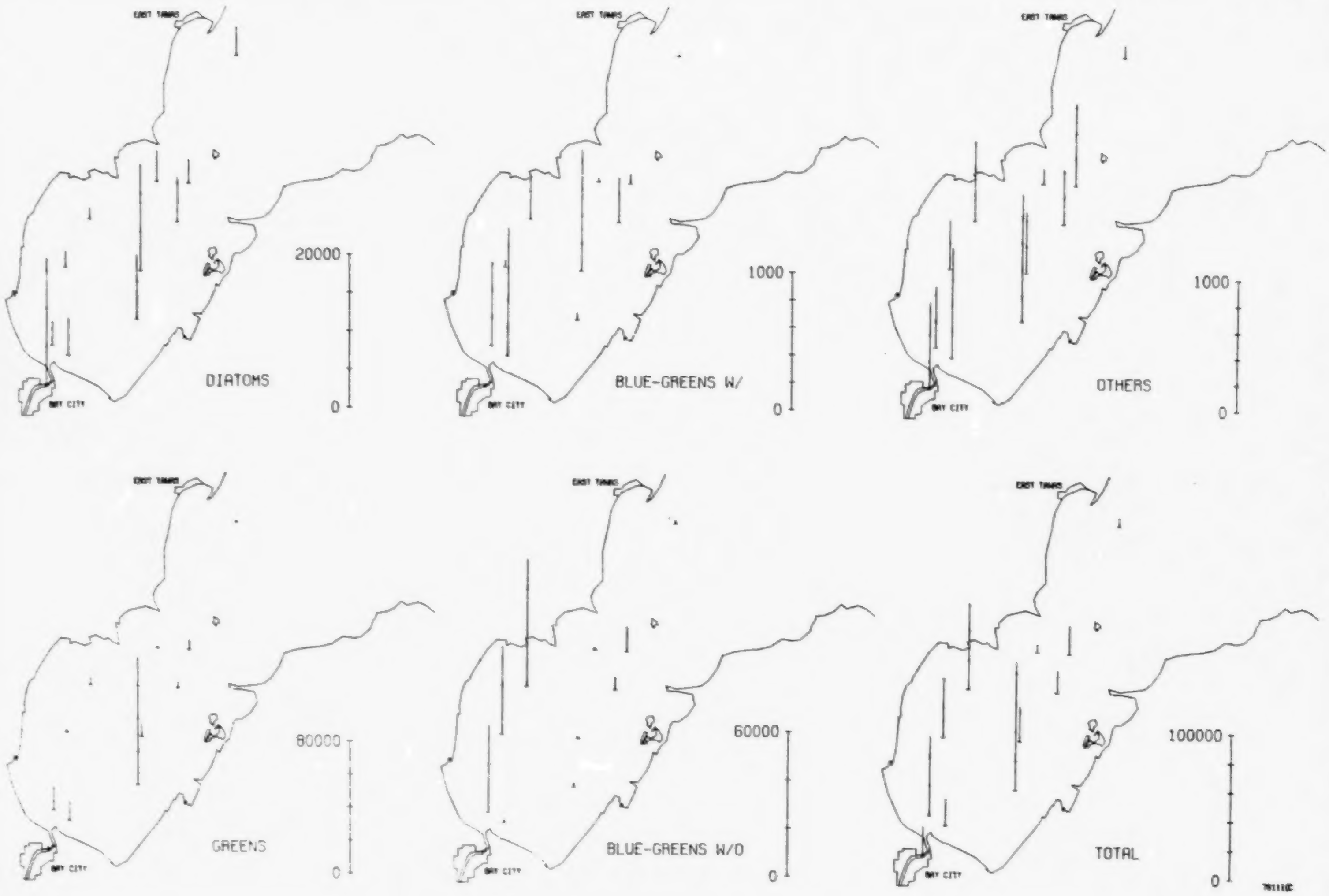

EAST TAWAS
BAY CITY
DIATOMS
30000
0
BLUE-GREENS W/
3000
0
OTHERS
2000
0
GREENS
15000
0
BLUE-GREENS W/O
80000
0
TOTAL
100000
0

Figure 40. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 7 October 1976.


EAST TAWAS
BAY CITY
DIATOMS
20000
0
BLUE-GREENS W/
1000
0
OTHERS
1000
0
GREENS
80000
0
BLUE-GREENS W/O
60000
0
TOTAL
100000
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761110C

Figure 41. Distribution of major phytoplankton groups in Saginaw Bay for cruise beginning 10 November 1976.

entire range of ecological adaptations found in the modern Great Lakes, with the exception of populations specifically adapted to very oligotrophic conditions. Part of this variability results from the large number of quasidiscrete habitats present within the bay. There are a large number of shallow, very productive areas which may produce local blooms of particular species which are later entrained into the general water mass and physically mixed with other populations. There are a number of examples of intense local blooms of particular populations at a particular station or at a few stations within a local region. This type of occurrence is most visible in the earlier sampling rounds which included more stations and particularly more stations relatively near to shore. The high productivity potential, particularly in the inner bay, can lead to extreme local differences in both the numbers and kinds of phytoplankton present. This extreme regional patchiness is one of the outstanding characteristics of phytoplankton distribution within the bay.

The overall diversity of the flora also partially results from the fact that the flora of the bay at any given point in time may be a composite of populations developed under different conditions. The most obvious source of atypical populations is Lake Huron. Under certain conditions it appears that the Lake Huron water mass extends a considerable distance into the bay. Apparent cases of this situation occurred in April, June, and September 1974 and July and October 1975. In these cases it appeared that a "wedge" of Lake Huron water extended into the bay. In other cases disjunct populations of species usually associated with the offshore waters of Lake Huron were noted at mid-bay stations. The only apparent explanation for such occurrences is that these populations were entrained in a deep-running counter current of Lake Huron water which entered the bay and subsequently welled up in the mid-bay region.

Another source of populations adapted to conditions at the other end of the spectrum of chemical conditions is the Saginaw River. In most cases studied, the flora of the river was dominated by species tolerant of highly eutrophic conditions and extremely high conservative ion concentrations. The most characteristic populations were several species of small centric diatoms, including *Cyclotella atomus*, *C. cryptica*, *Sceletonema potomos*, and *S. subsalsa*. The flora of the river was generally distinct from that of the open bay. It appears that populations in the river are rarely, if ever, nutrient limited. Large diatom populations were maintained throughout the summer and heterocyst forming blue-green algae were rarely abundant at stations in the river. In some instances, populations usually associated with the river were major dominants at stations in the vicinity of the river mouth and smaller numbers of these populations were occasionally found at stations throughout the lower bay.

A third source of assemblage heterogeneity particularly important in Saginaw Bay is the periodic entrainment of benthic populations. Although this mechanism is less well documented, it is quite probably an important factor in the ecology of the region because it furnishes a direct linkage between the sediment sink for nutrients and toxicants and planktonic food webs. Several distinctive types of populations are involved. The most conspicuous elements of this flora are large pennate diatoms. Some of the characteristic populations are *Caloneis amphisbaena*, *Nitzschia sigma*, *N. sigmoidea*, and several members of the *N. tryblionella* complex, *Surirella angusta*, *S. ovalis*, and several members of the *S. ovata* complex. Although these species are rarely numerical dominants, they are large cells and they may constitute an appreciable fraction of the biovolume at stations in the inner bay. They are all apparently tolerant of highly eutrophic conditions and high levels of conservative ion contamination. Although there is admittedly little direct evidence to demonstrate it, we also suspect that at least some of the filamentous green and blue-green algal populations which are dominant populations in the bay may be derived from benthic habitats. These populations occasionally have very erratic distribution patterns, especially early or late in the season. They also often contain abundant polyphosphate bodies, indicating growth under high nutrient and/or stress conditions.

Another group of organisms important in Saginaw Bay, with a similar type of meroplanktonic growth cycle, are several species of diatoms which have become noted indicators of eutrophication in the Great Lakes. Included in this group are species such as *Actinocyclus normanii* fo. *subsalsa* and *Melosira granulata*. These species are planktonic in the sense that they have no apparent special adaptation to benthic existence. They, however, are very heavy-walled forms. They also apparently have a relatively high temperature requirement in that they are generally most abundant in the summer and fall. Such species are usually not successful in the offshore waters of the Great Lakes because they are very susceptible to sinking losses, and nutrient supply is limited during summer stratification. They do become dominant populations in areas such as Saginaw Bay, lower Green Bay, and western Lake Erie. In these relatively shallow areas wind-induced mixing can furnish sufficient turbulence to resuspend populations and at the same time reentrain nutrients from the near bottom waters. Although it has not been widely reported in the literature, our results indicate that such populations may be able to store internal phosphorus, in the form of polyphosphate bodies, far in excess of their immediate requirements. The clearest evidence for this is found in *Fragilaria capucina*, another meroplanktonic species which is often a dominant form in highly enriched regions of the Great Lakes. It differs from the species discussed above in the fact that it is apparently tolerant of low temperatures and is usually most abundant during spring mixing. As discussed later, this species has a much larger fraction of its cellular volume in silica frustule than is the case with species such as *Stephanodiscus binderanus* and other euplanktonic forms which bloom under eutrophied conditions. Although *Fragilaria capucina* can store excess phosphate, its dispersion is limited by large sinking losses, except under ideal conditions. On the basis of our data, it appears that the dispersion of populations such as *Actinocyclus normanii* fo. *subsalsa* and *Melosira granulata* is even more limited, although they may be dominant populations in the bay under ideal conditions.

All of the above factors tend to modify phytoplankton responses to the overriding factor of extreme nutrient loading to the bay. It is clear that excessive phosphorus loads lead to silica limitation and consequent reduction in diatom growth during the summer. It is also clear that at least transient nitrogen limitation occurs, favoring the growth of heterocyst forming blue-green algae. On the basis of our results, however, it is apparent that physical events can act to de-couple nutrient loads from the directly expected physiological response of phytoplankton within the bay.

The general pattern of phytoplankton succession in the bay is less well defined than it is in more stable systems, but the following sequence appears to be characteristic. Phytoplankton assemblages in the bay are dominated by diatoms and flagellates during the winter circulation. Occasional populations of green and blue-green algae are noted, but these groups are generally a minor component of the total assemblage. With increased insolation during the spring, total phytoplankton abundance increases, forming the strong spring bloom characteristic of eutrophic systems. The timing of the maximum spring bloom appears to be variable from year to year and is undoubtedly controlled by the extent of ice cover in the bay and turbidity immediately following break-up of the seasonal ice cover. As soon as the water column begins to stabilize, the spring dominant diatom populations rapidly become silica limited, allowing increasing abundance of phytoplankton groups which do not require silica for reproduction. Phytoplankton succession then proceeds along the path from dominance by green algae and non-heterocyst-forming blue-green algae toward large populations of nitrogen-fixing blue-greens. It should be emphasized, however, that the timing of this sequence and the absolute "switch-over" of physiological groups characteristic of smaller hypereutrophic lakes is not so clear-cut in Saginaw Bay. In Saginaw Bay the normal course of events appears to be a return to a more mixed flora in the late summer and early fall. During this period three distinctive thermophilic diatom associations may develop in different regions of the bay. The Saginaw River and stations directly under the influence of its plume develop an association characterized by *Thalassiosira*, *Stephanodiscus*, and *Cyclotella* species tolerant of high temperature, high nutrient and conservative ion levels, and relatively high turbidity. The extent of penetration of these populations into the open waters of the bay is highly variable, but some species are commonly found at stations throughout the lower bay. The lower and mid-reaches of the bay develop a substantially different association, dominated by species of *Actinocyclus* and *Melosira*, as discussed earlier. In several instances late summer diatom blooms were also noted at stations in the Lake Huron interface region. Although assemblages in this region may contain some of the species found further down in the bay, they are generally dominated by blooms of *Cyclotella comensis*. This species has recently become much more abundant in the upper Great Lakes. In recent years massive, auxospore forming, summer blooms of this species have been noted in the Saginaw Bay interface and other relatively heavy-nutrient-load localities (e.g., Thunder Bay). The species has not been widely reported from the United States, but it apparently has a high nitrogen requirement and is especially efficient at uptake of silica at low concentrations.

The most plausible explanation for this somewhat atypical temporal sequence of major physiological groups is recycling of nutrients, particularly silica, which were earlier sequestered during the spring bloom. This explanation is supported by the results of Smith et al. (1977), which show a detectable increase in soluble reactive SiO_2 during late summer and early fall. Direct measurements of silica recycle from Saginaw Bay sediments

(J. A. Robbins, personal communication) show rates which are consistent with the hypothesis of substantial silica resupply during this period. It is interesting to note that this apparent nutrient resupply affects both the composition of the Saginaw Bay flora and the growth potential of populations more characteristic of open lake conditions which occur in the Saginaw Bay interface region.

One of the most crucial points in this investigation is the degree and intensity of effect on Lake Huron resulting from loadings and biological processes in Saginaw Bay. Our results indicate that substantial effects are present, but that the region and intensity of effect is highly variable.

In the average case it appears that the southern coast of Saginaw Bay is most strongly impacted and that export of phytoplankton populations associated with highly eutrophic conditions usually occurs through the region represented by the shoreward stations in region 5. This is the case which would be expected from consideration of circulation in the bay under average wind conditions (Allender, 1975; Danek and Saylor, 1977). As Danek and Saylor (1977) emphasized, actual circulation patterns within the bay are highly variable and show rapid response to both variations to forcing by ambient wind fields and the general circulation of Lake Huron. This instability is reflected by phytoplankton distribution. It is quite clear that meteorological conditions can have a strong influence on the eventual fate of materials entering the bay and on the fate of phytoplankton populations generated by nutrient loadings. In this context, further research should be devoted to the effects of conditions which force strong advective events on processes in Lake Huron. The results of Stoermer and Kreis (1980) are in agreement with our observations of typical distribution patterns in the Saginaw Bay-Lake Huron interface region. Their results show a general pattern of effects southward along the Michigan coast with large variations in the area of Lake Huron showing floristic similarities to Saginaw Bay. In one instance this general pattern is reversed with materials advected from Saginaw Bay apparently being dispersed northward. Their results also show that, under certain conditions, populations such as *Aphanizomenon flos-aquae* which were most probably generated in Saginaw Bay may be transported into the international waters of Lake Huron.

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SECTION 2

BIOMASS ESTIMATES

INTRODUCTION

Meaningful and reproducible estimation of phytoplankton biomass remains a remarkably complex problem. In the past few years, several investigators have returned to estimates of biovolume in an attempt to escape limitations of traditional secondary measurement techniques. Biovolume estimates based on species composition, number, and estimated volume have three inherent problems: (1) There is a lack of accuracy in measuring and computing volumes of microscopic, irregularly-shaped, complex forms; (2) There are differing amounts of metabolizing cytoplasm, vacular "dead" volume, and resistant wall materials found in different divisions of organisms commonly found in phytoplankton assemblages as well as in different species in any particular division; and (3) The physiological state of the cell (as a direct result of environmental conditions such as light, temperature, and nutrients, as well as the cell cycle of each organism) may affect both cell size and relative volumes of cytoplasmic constituents within the cell.

Electron microscopic morphometric methods are based on mathematical developments that consider the probability of obtaining certain two-dimensional profiles from three-dimensional structures by randomly cutting those structures. These methods are commonly used to detect quantitative differences in tissues and cells as an alternative to qualitative differences that might be noted during routine observation. During a study of phytoplankton populations from Saginaw Bay, it became evident that morphometric methods could be successfully applied to some members of the assemblage in order to arrive at volume estimates of components of ecological significance such as carbon-containing cytoplasm, chloroplast, and "inert" structures. We have utilized these methods to estimate the volume density of cellular components such as cell wall, chloroplast, vacuole (areas devoid of any discernible cytoplasmic components, including gullet, reservoirs, or furrows), storage products, and the remaining cytoplasmic components. The results of the study indicate that the problems associated with biovolume estimates can be both understood and, in many cases, minimized.

MATERIALS AND METHODS

All organisms examined in the morphometric analyses were obtained from nearshore Saginaw Bay field samples. Samples of _Anabaena_ _flos-aquae_ were collected from a surface bloom on 9 June 1975 at Station 18 (Lat. 43°44.5'N, Long. 83°46.4'W) approximately 8 mi from the western shore. All other samples were obtained from collections at Station 56 (Lat. 43°43.8'N, Long. 83°37.7'W) on 10 April 1975, approximately 4.5 mi offshore, and at Station 12 (Lat. 43°38.4'N, Long. 83°39.7'W) on 3 May 1975, approximately 2 mi offshore. Water chemistry values and phytoplankton species composition were similar for the two stations during the sampling periods in question. These samples were particularly well-suited for morphometric analysis since the major algal divisions were well represented in the samples and many of the taxa had high standing crops. Water was pumped from a depth of 1 m into 1-liter polyethylene bottles and was fixed immediately by adding sufficient glutaraldehyde (50%, biological grade) and sodium cacodylate to give a final concentration of 3% glutaraldehyde and 0.1M cacodylate at pH 7.2.

Samples were stored on ice and returned to the laboratory within 24 hr for further processing. Samples were then concentrated by gentle centrifugation and rinsed four times in 0.1M cacodylate buffer, pH 7.2. The concentrated cells were post-fixed with 1% OsO_4 in 0.1M cacodylate buffer for 1 hr at 4°C. Cells were then dehydrated in a graded ethanol-propylene oxide series and embedded in Epon (Luft, 1961). Thin sections for electron microscopy were cut with a diamond knife, collected on 300-mesh copper grids, and stained with uranyl acetate (Stempak and Ward, 1964) and lead citrate (Reynolds, 1963). Organisms were examined at a standard magnification of either 4,500X or 8,400X, depending on taxon cell size, using a Zeiss EM 9S-2 electron microscope. Magnification calibrations of the microscope were made by use of a replica grating to determine the stability of the standard magnifications. The variation was usually less than 2%. Specimens for total cell volume determination were fixed and dehydrated as outlined above, mounted in Epon on glass slides, and viewed using a Leitz Ortholux microscope equipped with a 95X oil-immersion objective, NA 1.30 or greater.

QUANTITATIVE STEREOLOGICAL METHODS

Eight taxa, including representatives from the classes Cyanophyceae, Bacillariophyceae, Euglenophyceae, Cryptophyceae, Dinophyceae, and Prymnesiophyceae (Hibberd, 1976), were selected for quantitative analysis. The sampling scheme employed was as outlined in Table 1. Seventy-five micrographs were examined for each taxon, except where scarcity of a particular taxon in the water samples necessitated a somewhat reduced sample size. In all cases, examination of coefficients of variation and plots of cumulative means and variances indicated adequate sampling of the material. A transparent 0.5-cm square sampling lattice was superimposed over the micrographs for quantitative measurements.

The first identifiable occurrence of each taxon on a grid was photographed. Identification or selection of organisms was not based on the presence or absence of particular cellular organelles. However, small grazing sections may be slightly undervalued in the samples due to problems associated with species identification. Blocks were retrimmed after each series of sections was cut, in order to avoid repeated sampling of adjacent material within the same organism. For filamentous taxa (eg. *F. capucina*, *S. binderanus*, *A. flos-aquae*), a single cell was randomly selected from each

TABLE 1. SAMPLING SCHEME EMPLOYED FOR MORPHOMETRIC ANALYSIS

	A. flos-aquae	S. binderanus	F. capucina	E. viridis	C. erosa	P. lindemanni	Hap 1	Hap 2
Number of Photos Examined	50	46	75	50	75	75	75	75
Final Magnification	25,100	13,600	25,100	13,600	25,100	13,600	25,100	25,100
Scope Magnification	8400X	4500X	84000	4500X	8400X	4500X	8400X	8400X
Photographic Enlargement	3.0X	3.0X	3.0X	3.0X	3.0X	3.0X	3.0X	3.0X
Average No. Pts/Photo	450	650	450	750	700	1500	450	250
Total Pts Counted	23,194	30,745	33,263	38,448	54,076	111,881	32,715	20,249

filament. The largest cross-sectional area of several of the taxa examined exceeded the photographic field of view at the standard magnification chosen. In these cases subsamples of the largest encountered cross-sections were photographed, using the upper left portion of the first such cell, the upper right portion of the next, the lower left, then the lower right, etc.

Estimates of volume density, i.e. the fractional volume of a cellular component related to its containing volume, were obtained using both the paper profile cut-and-weigh (Delesse, 1847) and grid point-counting (Glagoleff, 1933; Chalkley, 1943) techniques. Although both methods were found to yield similar estimates of volume density, point-counting was found to be easier and faster to implement. Except where specifically indicated, reported morphometric results will be those derived from the point-counting technique.

The point-counting method is an extension of the Delesse principle which states that the areal density of profiles on "two-dimensional" sections is an unbiased estimate of the volume density of the corresponding structures within the tissue (Delesse, 1847 cited in Weibel and Bolender, 1973), i.e.

$$\frac{V_i}{V_T} = \frac{A_i}{A_T} = \frac{P_i}{P_T} \qquad (1)$$

where V_i = volume of a component i, A_i = area of i in section, P_i = number of points falling within the boundary of i, V_T = total containing volume, etc. (Notation and definitions are those of Weibel and Bolender, 1973). Thus, by counting points of a sampling grid striking component i, or by weighing the area of _i_ on a two-dimensional section and comparing that quantity with a containing area measured in the same units, an unbiased estimate of the volume fraction of component _i_ in the original tissue can be obtained. Additional information concerning the more theoretical aspects of stereology can be found in one of the several excellent reviews on the subject (Loud, 1968; Underwood, 1970; Weibel and Bolender, 1973).

Actual cell volume estimates (μm^3) were obtained from light microscopic examination of cells obtained from the same assemblages as those used for the quantitative stereological analysis. Estimates are based on 10 independent measurements for each taxon, and assume a regular geometric shape for the taxon (Table 2). Specific geometric formulae used in the volume calculations are also presented there.

Statistical analyses were performed with the assistance of the MIDAS statistical routines available through the computing facilities at the University of Michigan. Parameter estimates are reported as the mean ± 1 standard error unless specifically designated otherwise.

TYPING GUIDE SHEET

TABLE 2. CELL VOLUME ESTIMATES FOR THE EIGHT PHYTOPLANKTON SPECIES EXAMINED
b = breadth, l = length, h = height, d = diameter

TAXON	Volume μm^3	(SE)	Formula
Anabaena flos-aquae	80	(9)	$1/4\pi d^2 h$
Stephanodiscus binderanus	830	(92)	$1/4\pi d^2 h$
Fragilaria capucina	400	(37)	blh
Euglena viridis	3100	(450)	$1/6\pi l_1 b_1^2 + 1/4\pi l_2 b_2^{2*}$
Cryptomonas erosa	1300	(250)	$1/6\pi l b^2$
Peridinium lindemanni	11000	(2100)	$1/8\pi l b^{2\dagger}$
Haptophyte 1	100	(20)	$1/4\pi d^2 h$
Haptophyte 2	70	(7)	$1/4\pi d^2 h$

***Euglena* was assumed to be a composite geometric shape consisting of a rotation ellipsoid with major axis of rotation l, and minor axis b, and a smaller cylinder of height l_2 and average diameter of b_2.

†*Peridinium* was assumed to be intermediate in volume between a rotation ellipsoid with major axis of rotation l and a composite shape consisting of two cones each of height $l/2$.

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RESULTS AND DISCUSSION

DESCRIPTIVE ELECTRON MICROSCOPY

The following is a brief description of each of the organisms involved in this study, with detailed information presented on the ultrastructure of the organism and how this information can be correlated with physiological evidence.

Anabaena flos-aquae (Cyanophyceae)

The blue-green alga, *Anabaena flos-aquae*, was selected to be a representative nitrogen-fixing organism. The organism was collected as a surface bloom with the cells forming tangled masses (Fig. 1). The cells are cylindrical to spherical; the heterocysts are usually terminal (Fig. 2).

Blue-green algae are quite distinct, cytologically, from other algal groups. This is due to the fact that they are prokaryotic, and hence, more closely aligned with bacteria both in structure and physiology. At the light microscope level, the structural features that can be observed in the blue-green algae are the centroplasm or nucleoplasm, the central portion of the cell which is rich in nucleic acids, and the chromatoplasm, the peripheral portion of the cell that contains the photosynthetic pigments and several types of granules. With the aid of the electron microscope (Figs. 3, 4), greater resolution of these features is achieved. The categories of cellular compartments in the blue-green algae that were included in quantitative electron microscopy were as follows:

Cell Wall--

This consists of four layers, including the peptidoglycan (including muramic and diaminapimelic acids). Dunn et al. (1971) have estimated that 10 - 20% of the dry weight of *Anabaena cylindrica* is wall material (exclusive of mucilage or sheath). For the present study, mucilage was not included in cell wall volume determinations, since very little was present.

"Pseudovacuole"--

The category pseudovacuole in this study collectively refers to both areas of intrathylakoidal spaces as well as areas of collapsed gas vacuoles. The intrathylakoidal spaces may be either fixation artifacts (since the cells were fixed in glutaraldehyde, not the method of choice for prokaryotes) or real spaces, as these areas can form under certain nutrient conditions (Jensen and Sicko, 1974; Sicko, 1974). At best, the estimation of vacuolar space in the blue-green alga is an approximation, since the vesicles were collapsed. Van Baalen and Brown (1969) and Smith and Peat (1967) have shown that gas vacuoles may take up as much as 60-70% of the total cell volume. Gas vacuoles have been demonstrated to be formed when the algae are subjected to ionic deficiency (Waaland and Branton, 1969). In addition to regulating buoyancy and consequently environmental conditions, gas vacuoles may also be a means for concentrating ions within cells by decreasing intracellular solution volume.

KEY TO FIGURE LEGENDS

c - cyanophycin granule
cl - chloroplast
cy - cytoplasm
cw - cell wall

e - ejectosome

f - frustule

g - golgi body
gb - girdle band
gu - gullet
gv - gas vacuole

h - heterocyst
ha - haptonema

l - lipid

m - mitochonchia
mt - microtubules

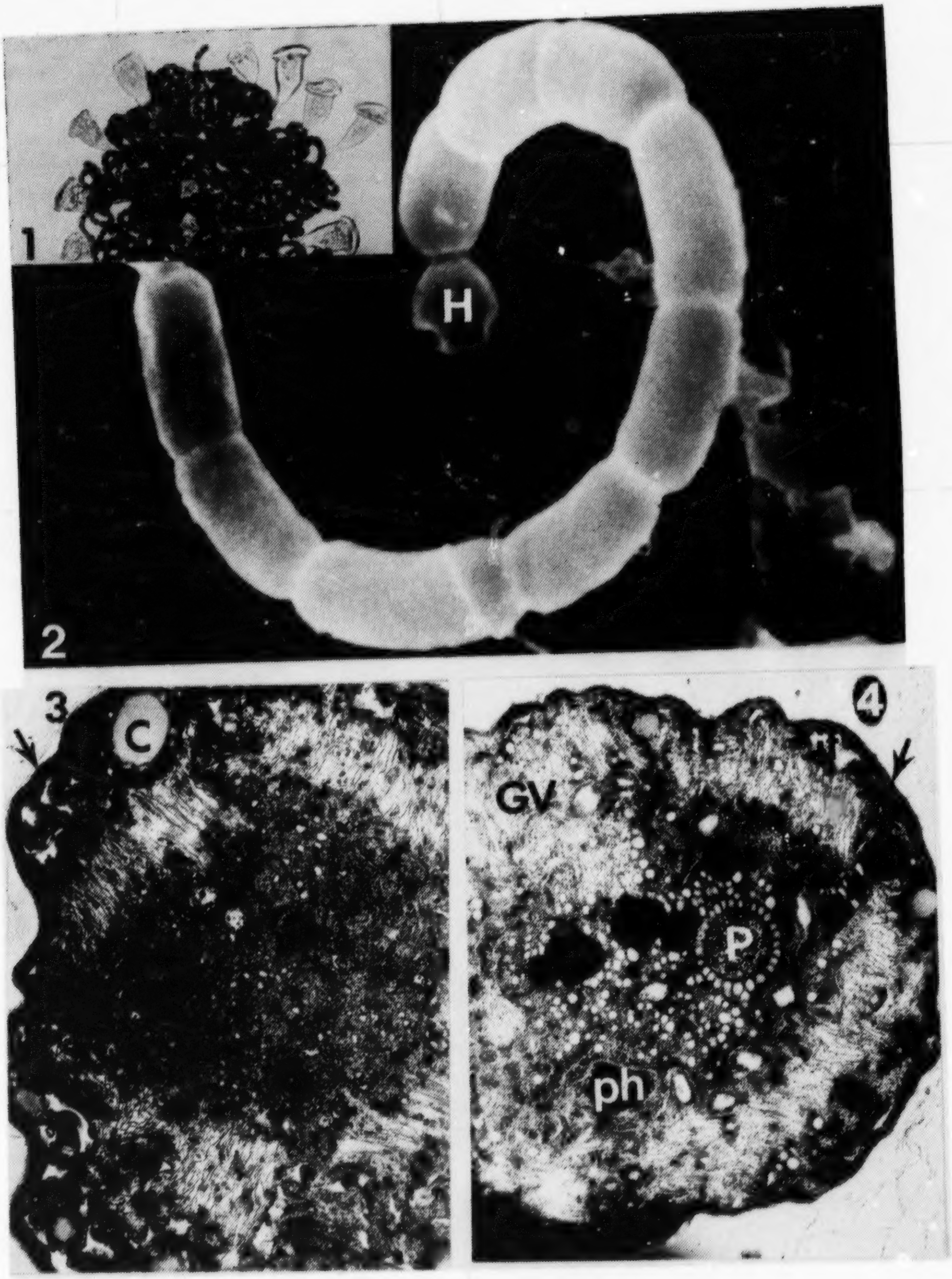
n - nucleus

p - polyphosphate body
ph - polyhedial body
pa - paramylon
pe - pellicle
py - pyrenoid

s - storage body
su - sulcus
st - suture
sr - starch

t - trichocyst
tp - thecal plate

v - valve
vac- vacuole


1
H
2
3
C
4
GV
P
ph

Figures 1-4. *Anabaena flos-aquae*
1. X250
2. X8,600
3. X18,800
4. X27,300

Nitrogen Storage--

Cyanophycin granules or structured granules are present in both vegetative cells and akinetes of blue-green algae. They consist of high molecular weight copolymers of aspartic acid and arginine (1:1, mol/mol). This extremely unusual composition reveals them as particularly well suited to serve as a nitrogen reserve (Simon, 1971a). Simon (1971b) isolated these granules from nitrate-grown vegetative cells of Anabaena cylindrica, where they account for up to 10% of the dry weight.

Phosphate Storage--

Polyphosphate bodies are present in limited numbers in blue-green algae unless the algae are subjected to adverse nutrient conditions. Any type of nutrient imbalance can induce their formation, whether it be the presence of excess or absence of a particular nutrient. The polyphosphate bodies encountered in A. flos-aquae were limited in number and, for the most part, appeared extracted. This again is most likely a result of inappropriate fixation.

Cytoplasm--

The remaining components in the blue-green algae were collectively counted as cytoplasm. These include the nuclear area, ribosomes, "ground substance," polyhedral bodies, and thylakoids. No attempt was made to estimate the thylakoid volume as a separate category comparable to chloroplast.

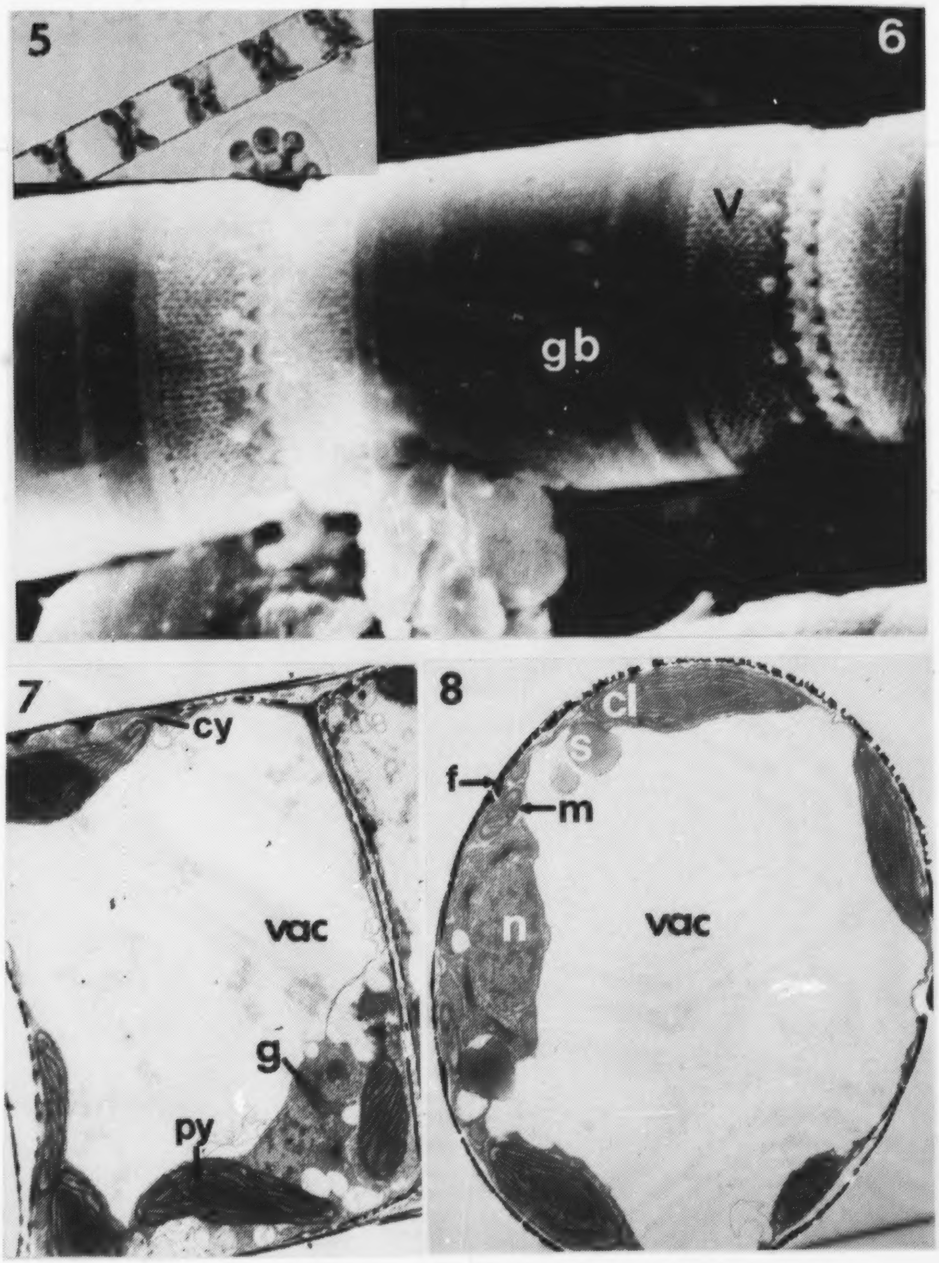
Stephanodiscus binderanus and Fragilaria capucina (Bacilliarophyceae)

Fragilaria capucina is primarily benthic in habitat preference, but it is also a successful facultative plankton. In samples analyzed, F. capucina (Figs. 9-11) was one of the most abundant organisms. Stephanodiscus binderanus (Figs. 5-8) is a euplanktonic species; it was not as abundant as F. capucina in the samples examined.

The diatoms are most distinct at the ultrastructural level. This is due to the siliceous wall or frustule. This same feature (i.e., the siliceous frustule) also makes diatoms one of the most difficult algal groups to study at the ultrastructural level because the frustule is very hard, making thin sectioning difficult. In general, each cell contains two or more chloroplasts, a nucleus, either a central or two polar vacuoles, mitochondria, golgi, ribosomes, and endoplasmic reticulum. The following celular categories were included in the diatom morphometric analysis:

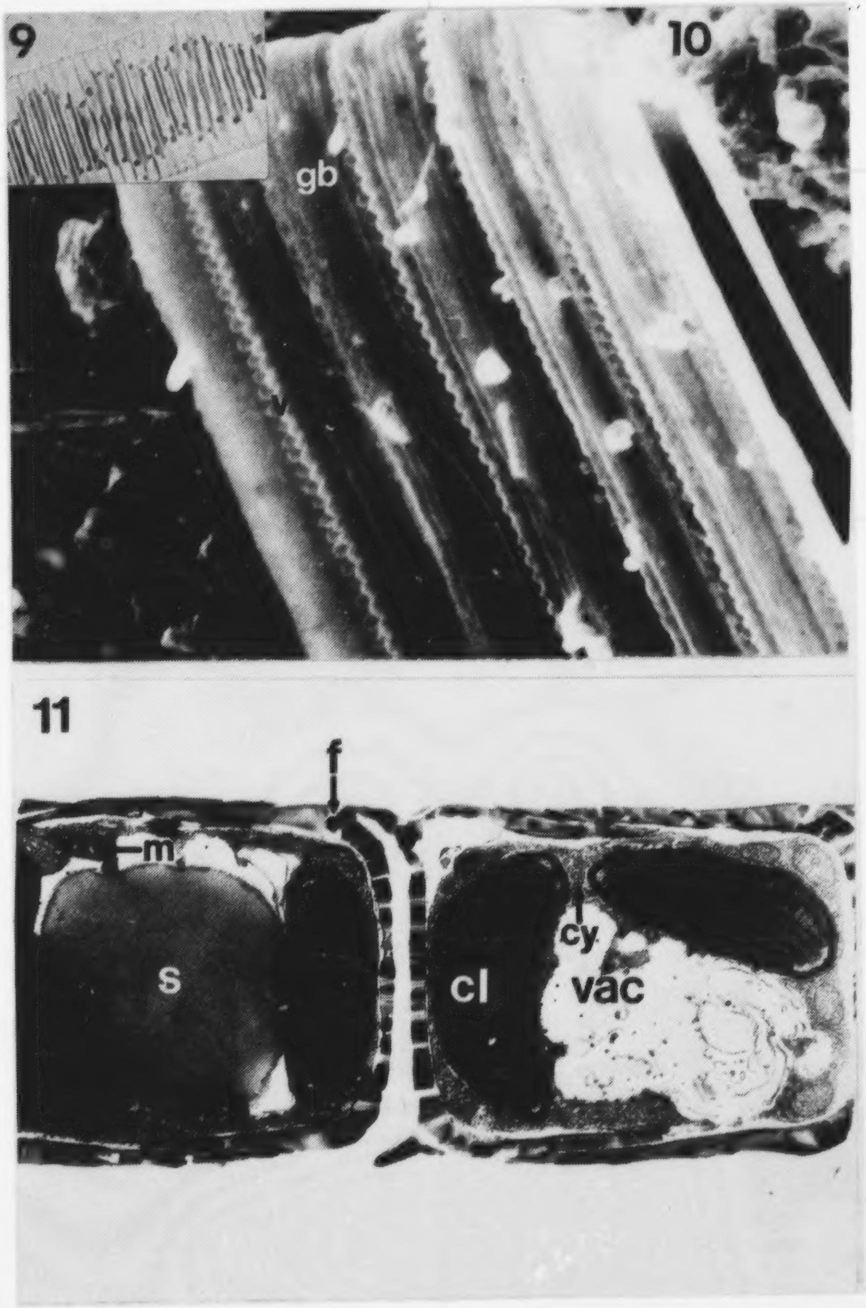
Frustule--

The frustules of the two diatoms examined differed significantly in thickness (Figs. 7, 8, 11). The frustule is easily identified in electron micrographs as electron dense material, platelike in nature, immediately outside the plasma membrane. Lewin and Guillard (1963) point out that the variation in frustule thickness is both intraspecific and interspecific, ranging generally between 4 and 50%. Because of this variation, estimates of organic constituents on a dry weight basis from total cell volume estimates are of doubtful value, and not easily compared with other algal groups.


5
6
V
gb
7
cy
vac
g
py
8
cl
s
f
m
n
vac

Figures 5-8. *Stephanodiscus binderanus*

5. X980
6. X10,000
7. X10,000
8. X9,050


9
10
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vac

Figures 9-11. *Fragilaria capucina*
9. X750
10. X8,250
11. X18,200

Vacuole--

Vacuoles in diatoms are variable. In *S. binderanus* (Figs. 7, 8) the large central vacuole restricts cytoplasmic organelles to the periphery of the cell. This situation is not common in diatoms, having only been reported in *Melosira varians* (Crawford, 1973). In *F. capucina*, the vacuolar arrangement is similar to other naviculoid diatoms, in that the cytoplasm is H-shaped, with parietal chloroplasts and a central cytoplasmic bridge (Stoermer et al., 1965; Drum, 1963; Dawson, 1973). Storage products, usually lipids, are often found within the vacuolar membrane (tonoplast).

Storage Products--

The storage product most commonly encountered in both diatoms appeared to be lipid, located mainly in the vacuoles (Figs. 8, 11). As with many other algae, storage products accumulate in older cells (Crawford, 1973; Lewin and Guillard, 1963). It has been demonstrated that, in young diatom cultures, lipids constitute 5-15% of the dry weight, whereas in N-deficient cultures it may increase to 40-50%.

Chloroplast--

The chloroplasts in both diatom species examined here are similar structurally to those described in other diatoms. The plastids are bounded by an envelope composed of two membranes, which in turn is surrounded by a membrane of endoplasmic reticulum (ER). The plastids contain pyrenoids which are traversed by a single lamella, composed of three thylakoids. In the morphometric analysis, the pyrenoid was counted in two categories, total chloroplast and chloroplast storage. In the final analysis, the pyrenoid point totals were added to the total storage, since it is believed to be involved in the conversion and translocation of early photosynthate in chloroplasts (Griffith, 1970). This function would more closely align it with storage than with chlorophyll content.

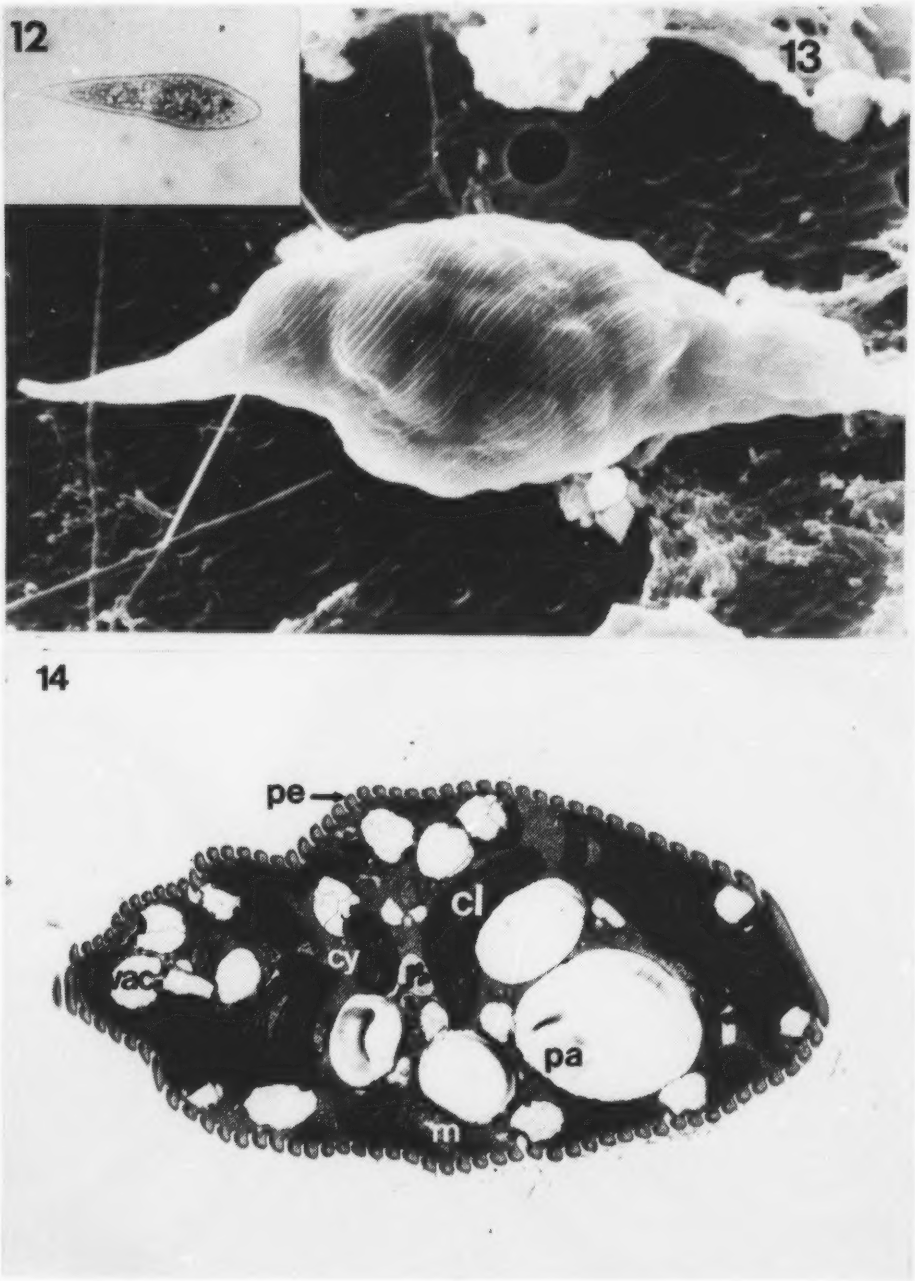
Cytoplasm--

Other eukaryotic cell organelles included in this category and in none of those previously mentioned include nucleus, golgi, ribosomes, mitochondria, and "ground substance."

Euglena viridis (Euglenophyceae)

Cell Wall--

In *Euglena* (Fig. 12), the cell covering is a unique structure termed the pellicle (Figs. 13, 14). The pellicle is believed to consist of several components: 1. plasma membrane, 2. protein layers beneath and parallel to the plasma membrane, 3. microtubules, and 4. an endoplasmic reticulum cisterna. It has been demonstrated (Barras and Stone, 1965) that the pellicle is composed of approximately 80% protein. Silverman and Hikida (1976) demonstrated that the pellicle of *E. gracilis* was highly resistant to disruptive treatment, and speculate that the proteins and microtubules in the distinct pellicle ridges (Fig. 14) perform a cytoskeletal role. For the purpose of this study, the area counted in the "wall" category included the points


12
13
14
pe
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cy
vac
pa
m

Figures 12-14. Euglena veridis
12. X1,060
13. X5,280
14. X12,100

between the ER cisterna and the external surface of the cell. This area constitutes the easily identifiable ridge.

Vacuole--

The structures in Euglena which, perhaps, are most closely aligned with the vacuole in the other algae examined are the anterior canal, reservoir, and contractile vacuole (Fig. 14). The subapical anterior invagination of the cell from which the flagella emerge is the anterior canal; the flagella have their bases in the reservoir. The contractile vacuole is located adjacent to the reservoir on the side opposite the eyespot. Since Euglena is a naked cell, in fresh water it is subject to continuous uptake of water by osmosis. To prevent the cell from bursting and to enable it to maintain its normal size and shape, water must be discharged. At discharge, the membrane between the contractile vacuole and reservoir breaks down, with the water from the contractile vacuole emptying into the reservoir. This entire area is surrounded by microtubules, believed to function in closing the canal (Leedale et al., 1965). Since this area is obviously osmo-regulatory in function, and contains no discernible organic components within the membranes (disregarding the flagella), it was counted in a category comparable to vacuole in other organisms.

Storage Products--

The reserve polysaccharide of Euglena is paramylon. It consists solely of $\beta(1 \rightarrow 3)$ linked D-glucose residues and occurs as water insoluble single membrane-bound inclusions (Craigie, 1974). Carbon starvation of Euglena results in the rapid disappearance of paramylon; restoration of a carbon source leads to a complete reversal to normal morphology (Malkoff and Buetow, 1964; Leedale and Buetow, 1970). The degradation of paramylon is photoregulated (Schwartzbach et al., 1975). In the presence of sufficient nutrients and no light, carbon is used for cell growth. When light is the major energy source and no external carbon is supplied, paramylon is degraded. This degradation ensures sufficient carbon and energy for plastid development when the cells are exposed to light.

Chloroplast--

Euglena generally contains numerous chloroplasts. The chloroplasts contain thylakoids which are not arranged as grana; pyrenoids are absent.

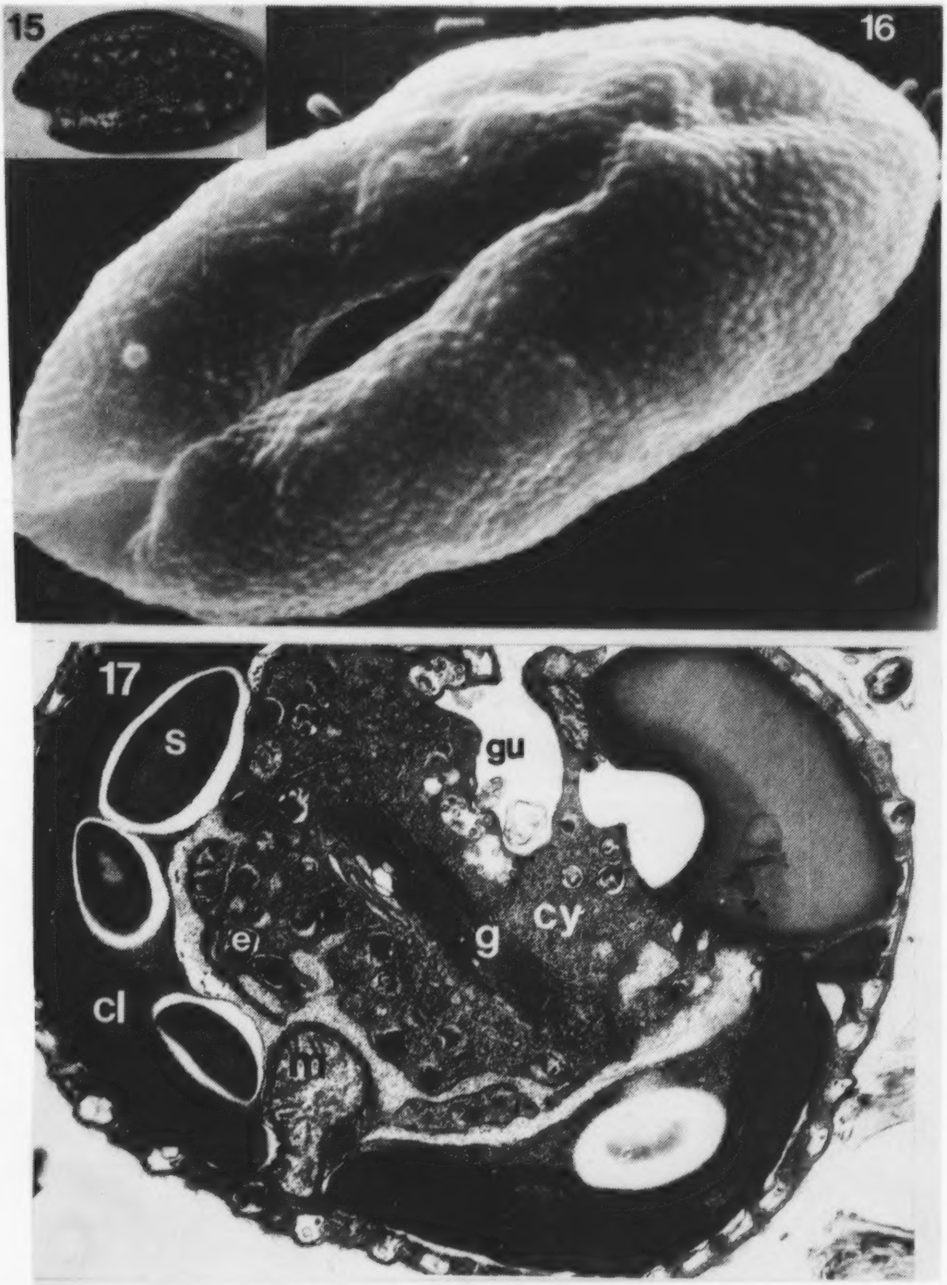
Cytoplasm--

Other organelles included in this category were nucleus, golgi, mitochondria, endoplasmic reticulum, ribsomes, and eyespot (adjacent to the reservoir).

Cryptomonas erosa (Cryptophyceae)

Cell Wall--

The cells of Cryptomonas (Figs. 15-17) are bounded by a single membrane which is regularly indented. The foldings or indentations on the surface are a result of the periplastial trichocysts (Gantt, 1971). The trichocysts themselves are contained within single membrane-bound vesicles and are not


15
16
17
s
gu
cy
g
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cl
m

Figures 15-17. *Cryptomonas erosa*
15. X2,130
16. X12,300
17. X22,900

generally considered part of the periplast. Since the wall is essentially a membrane, no estimation was made of its volume component.

Vacuole--
The area included in the morphometric analysis as vacuole in *Cryptomonas* roughly corresponds to similar structures in *Euglena*, namely, an anterior furrow from which the flagella emerge (Figs. 15, 16), a gullet (Fig. 17) comparable to, but not identical with, the reservoir, and a contractile vacuole or a series of small vacuoles of unknown function. Since these areas do not appear to contain any organelles or inclusions, the area point totals were equated with vacuole in other algae.

Storage Product--
The main storage product in *Cryptomonas* is starch. The starch generally occupies a position between the chloroplast envelope and the endoplasmic reticulum which encloses the chloroplast (Fig. 17). It appears as a polysaccharide cap around the pyrenoid, but is not actually part of the chloroplast (Dodge, 1969; 1973).

Chloroplast--
Cryptomonas contains two parietal chloroplasts. These chloroplasts contain many lamellae which consist of two thylakoids. The pyrenoid is most often not large, and is of the stalked variety (Dodge, 1973).

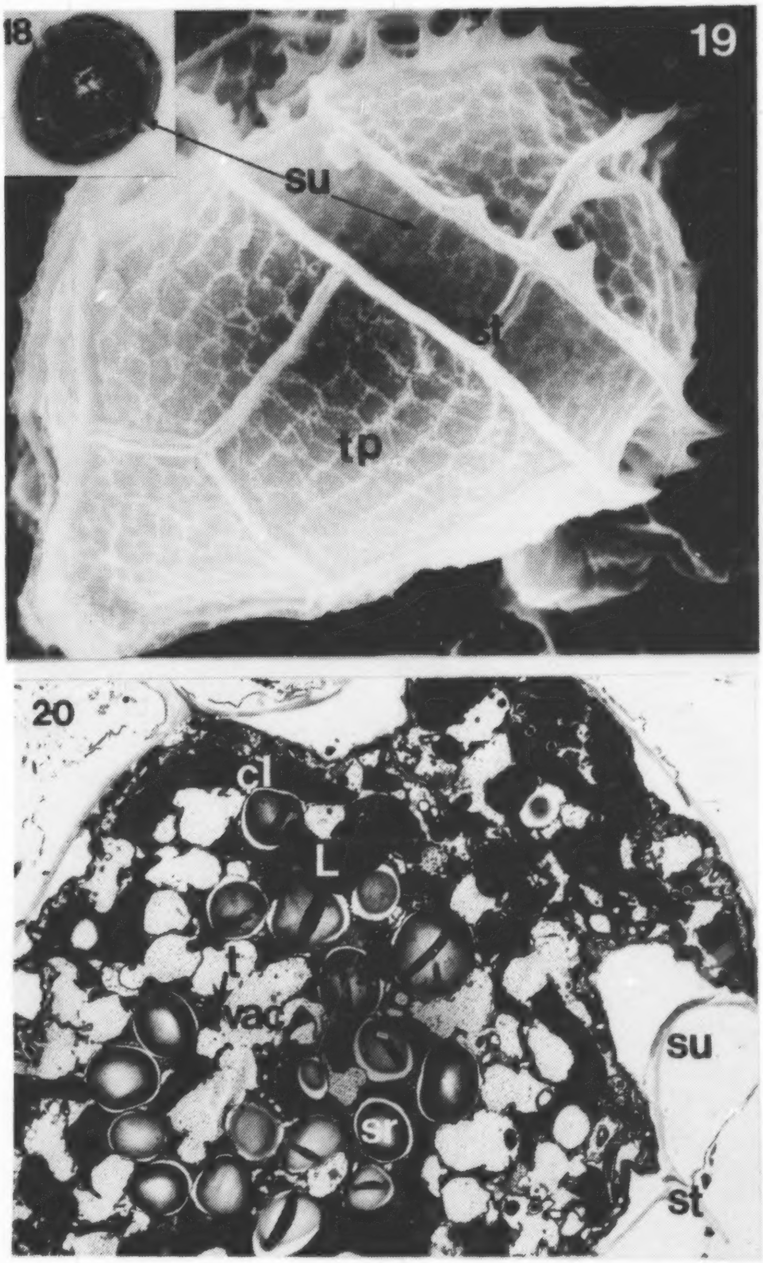
Cytoplasm--
The remaining cytoplasmic components in this category include golgi, mitochondria, ribosomes, "ground substance," and ejectosomes.

Peridinium lindemanni (Dinophyceae)

Peridinium lindemanni (Figs. 18-20) was found in large numbers in the April station selected for analysis. It also proved to be fairly abundant, though not in as large numbers in the May sample. The cellular components analyzed were the following:

Cell Wall--
The dinoflagellates possess a complex cell covering termed the theca or amphiesma (Loeblich, 1970). The theca consists of an outer membrane, flattened vesicles or thecal plates, and an inner membrane (Fig. 20). There are often subthecal microtubules which are sometimes evenly dispersed and arranged in pairs (Dodge, 1971). The thecal plates are organic in nature; thick microfibrils appear to be the main component and show random orientation (Dodge, 1965). At division, dinoflagellates share old plates, then synthesize new plates to complete their theca. Thus, it is possible to differentiate between newly divided and more mature cells (Dodge, 1971).

Vacuole--
Two types of vacuole or vacuole-like areas are commonly found in dinoflagellates, food vacuoles, and the pusule. Food vacuoles, either empty or with recognizable substances, have been described in *Ceratium* (Dodge and Crawford, 1970) and *Oxyrrhis* (Dodge and Crawford, 1974). The pusule is a


18
19
su
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Figures 18-20. Peridinium lindemanni
18. X810
19. X6,960
20. X6,540

unique osmo-regulatory organelle found in all freshwater dinoflagellate species examined (Dodge, 1972). It consists of vesicles, collecting chambers, and canals, and is more highly organized than contractile vacuoles of other common phytoplankton organisms. In P. lindemanni, the cells were highly vacuolated (Fig. 20), although the exact nature of the vacuoles was not determined.

Storage Products--

The main storage products (Fig. 20) of dinoflagellates are fats or oils, stored in the form of droplets, and starch grains (Dodge, 1973). The storage products are particularly abundant in organisms that have been fixed from a natural habitat in which the conditions were very favorable for photosynthesis (Dodge and Crawford, 1970).

Chloroplast--

The dinoflagellate chloroplast is typically bounded by a three membrane envelope which does not normally have any connections with other cellular constituents. The lamellae are made of stacks of three thylakoids, but there is some variability in the arrangement of the lamellae. As with other Peridinium species (Dodge, 1975), the chloroplasts in P. lindemanni are discoid (lens-like) in shape, have a radial orientation, are numerous, and are scattered throughout the cell (Fig. 20). The pryenoids encountered in Peridinium were small and not easily distinguished due to their location in the chloroplast lamellae. Consequently no attempt was made to quantitate their relative volume.

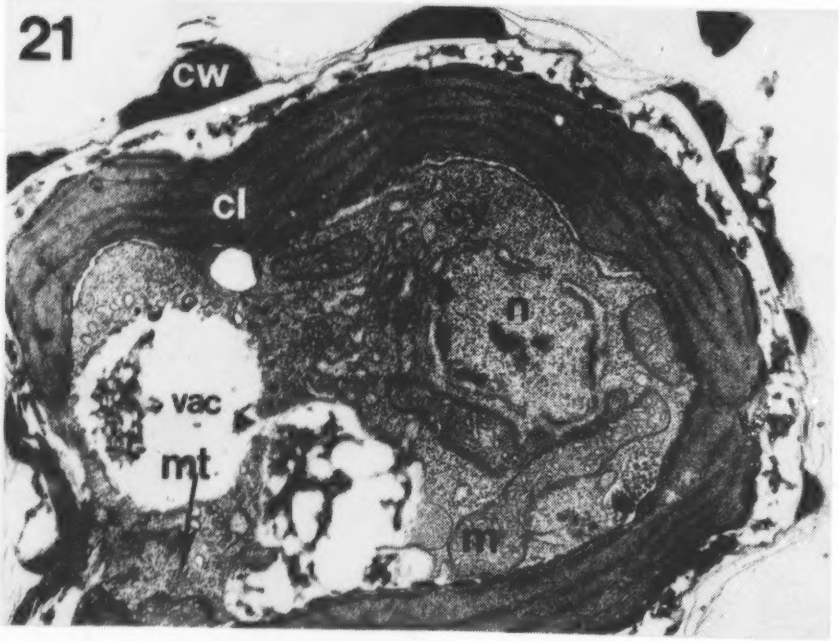
Cytoplasm--

Other organelles included in the cytoplasm category were nucleus, eyespot, trichocysts, mitochondria, golgi, ER, ribosomes, and "ground substance."

Prymnesiophycean Algae - Two Undetermined Species

A large number of small flagellates were encountered in the two stations selected for analysis. Although their identification is still undetermined, we have concluded that they are prymnesiophycean (haptophycean) algae based on several ultrastructural observations, all of which are characteristic of this group (Leadbeater, 1971; Manton and Peterfi, 1969; Hibberd, 1976).

1. Oftentimes, sections were taken through three flagella-like basal body areas.
2. Haptonemas were encountered in cross section in several pictures (a haptonema is a flagellar-like appendage, consisting of six or seven (Fig. 22) microtubles, and endoplasmic reticulum [Manton, 1964]).
3. The golgi apparatus is extensive, with dilated cisternae and numerous "hairy" vesicles.


21
cw
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n
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Figure 21. Haptophyte #1 X25,700

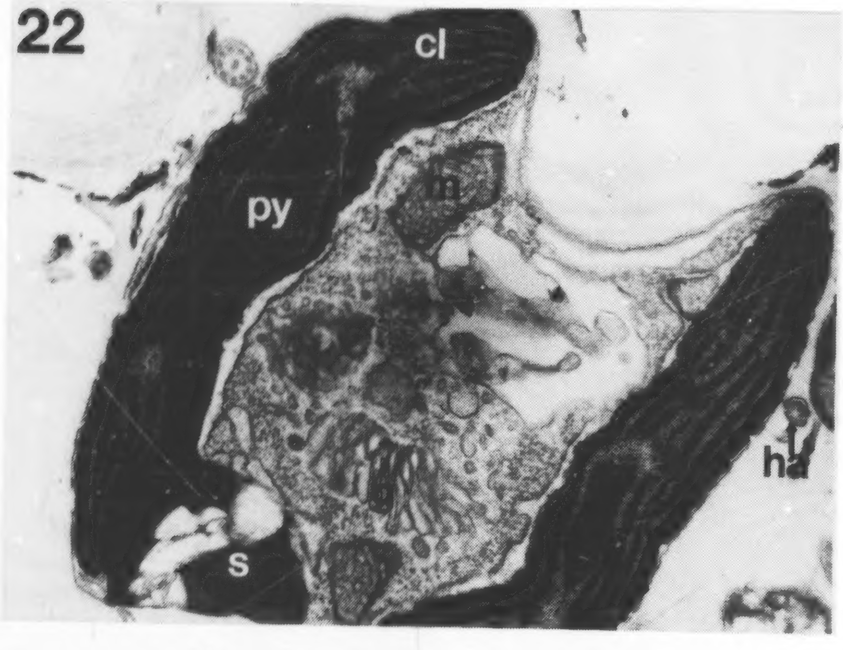
22
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Figure 22. Haptophyte #2 X31,500

4. At least one of the species (Fig. 21) has unmineralized scales (confirmed by X-ray energy dispersive analysis). The scales are obvious in all sections taken through the organisms. There is also a slight suggestion that the other species might also possess scales, although the freqency of such observations was considerably less. When scales were found externally, it was also possible to observe scales developing in the golgi.

5. Hexagonal arrays of microtubules were also found in sections near the flagellar apparatus and in close association with the chloroplast at the apical end of the cell, opposite the nucleus.

The two algae were selected for analysis because they represent both naked and scaled forms of the group. The following areas were defined for the morphometric analysis.

Cell Wall--
The cell wall was defined as the area outside the plasma membrane. For species #1 (Fig. 21), this consisted of the unmineralized scales, and dense osmiophilic bodies. The nature of these bodies is unknown. Since species #2 (Fig. 20) was naked, no wall points were counted.

Vacuole--
Clear areas devoid of cytoplasm were usually encountered in the cellular region adjacent to the flagellar apparatus. The amount of vacuole observed was highly dependent on section angle, indicating a small, polar vacuole.

Storage Products--
Chrysophycean algae store fat and chrysolaminarin, a $\beta(1 \rightarrow 3)$ linked glucan. These products have not been identified with any certainty in the Prymnesiophyceae (Hibberd, 1976). Thus for the purpose of analysis, lipid-like inclusions were counted as storage products.

Chloroplasts--
The two prymnesiophycean algae have two parietal chloroplasts per cell. The pyrenoid is embedded in the chloroplast with no thylakoid lamellae penetration. The lamellae have three thylakoids.

Cytoplasm--
Other organelles included in this category were ribsomes, endoplasmic reticulum, mitochondria, "ground substance," nucleus, flagellar apparatus, and the extensive golgi system and vesicles.

Quantitative Electron Microscopy

Sample Size Determination--
Plots of the cumulative mean and variance as a function of the number of micrographs examined were used to evaluate the adequacy of the micrograph sample size used in the morphometric analysis (Chalkley, 1943). The order of micrographs was randomized prior to mean calculation and plotting. Micrographs were then re-randomized and plotted a second time to check that

the plateau observed for the mean or variance was in fact stable and not a function of the order of micrographs. The cumulative means for the largest organism studied, *P. lindemanni*, and the smallest, *Haptophyte* sp#1, are presented in Fig. 23. Such plots demonstrate that the apparent requisite sample size will differ from organism to organism and from component to component within a given organism. Components that tend to be highly oriented, such as the Haptophyte chloroplast or vacuole, require a large number of random sections to characterize their volume fraction; components that tend to be more uniformly dispersed throughout the cell, e.g., the dinoflagellate chloroplast, seem to stabilize rather quickly. Most cellular components for the organisms examined in this study were adequately characterized by 30-50 random micrographs.

Filament Analysis

A preliminary pilot survey utilizing stereological cut-and-weigh techniques was undertaken to evaluate the bias introduced by sampling more than one cell from a given filament. Two factors suggest a possible bias in selecting cells from the same filament: (1) cells in a given filament are genetically and developmentally related; and (2) since cells in the same filament have been sectioned at the same angle, the primary stereological assumption of randomness of sectioning angle has been violated. However, since ease of sampling favors multiple samples from a single filament, the question was examined statistically.

Fifty-two electron micrographs -- representing 13 filaments of the diatom *F. capucina*, with four adjacent cells sampled per filament -- were measured using the stereological cut-and-weigh technique. The volume fractions obtained for frustule, storage, and cytoplasm for each of the thirteen filaments were compared using a one-way univariate analysis of variance (four replicates per ANOVA cell). The results are summarized in Table 3. All three analyses indicate that the between-filament variance is significantly larger than within-filament variance. Examination of mean cellular volume fractions for the 52 micrographs compared with means obtained from a sample of 13 micrographs, one randomly chosen from each filament, shows little difference between the two parameter estimates. Therefore, preliminary evidence seems to indicate that multiple samples from a single filament do not substantially improve volume estimates for the given filament and may potentially bias the population estimate if differing numbers of cells are sampled per filament.

General Descriptive Measures

The quantitative results presented in this study describe both physical and physiological "compartments" of the cell. In general, the following categories and their limits have been utilized:

*1. WALL/FRUSTULE = area outside of the plasma membrane.

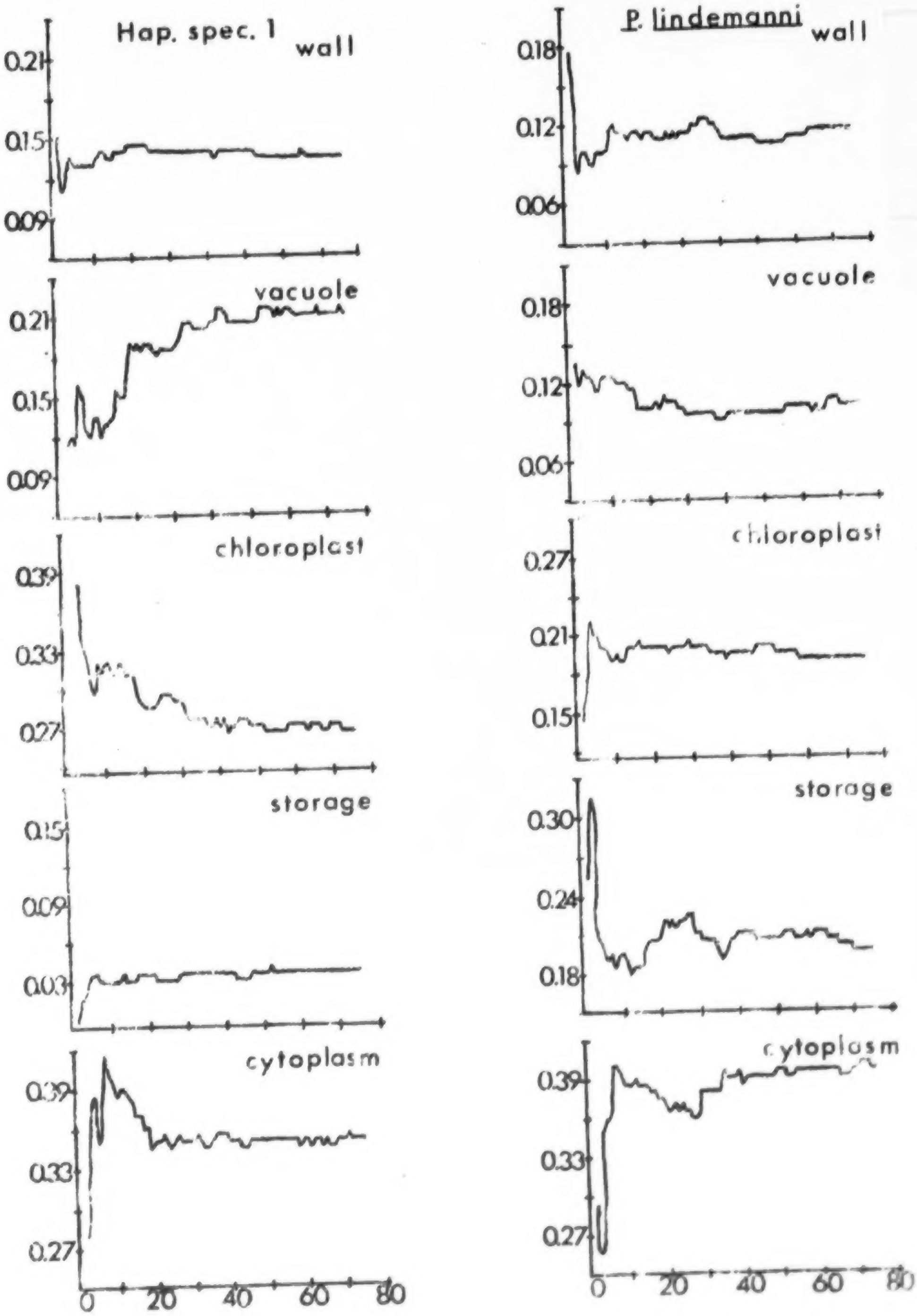

Figure 23. Cumulative mean (percent volume) as a function of sample size (number of micrographs) for five cytoplasmic components of P. lindemanni and Hap. 1.

TABLE 3. ANALYSIS OF VARIANCE (ANOVA) OF BETWEEN AND WITHIN FILAMENT VARIANCE

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F-STAT
Anova -- Frustule fraction				
Between filaments	12	.11900	.0099167	10.620*
Within filaments	39	.036417	.0093377	
Anova -- Storage fraction				
Between filaments	12	1.0297	.085811	89.631*
Within filaments	39	.037337	.00095737	
Anova -- Cytoplasmic fraction				
Between filaments	12	1.3666	.11388	29.381*
Within filaments	39	.15117	.0038762	

*Significant at .001 level

*2. VACUOLE = vacuole area of the cell bounded by the vacuolar membrane (tonoplast). This category may also include storage located in this region.

2a. VACUOLE STORAGE = that portion of the total vacuole volume which is storage (generally lipids in the diatoms).

2b. "EMPTY" VACUOLE = total vacuole - vacuole storage.

*3. CHLOROPLAST = chloroplast volume; also includes any pyrenoid and chloroplast storage products such as lipids and starch, if they are present.

3a. CHLOROPLAST STORAGE = storage within the chloroplast; pyrenoid plus starch.

3b. TOTAL CHLOROPLAST - CHLOROPLAST STORAGE.

*4. CYTOPLASMIC STORAGE = storage material (starch, lipids, oils, paramylon, etc.) located in the cytoplasm. Does not include vacuole or chloroplast storage.

*5. CYTOPLASM = all cellular components not included in one of the above categories (includes organelles such as golgi, nucleus, ejectosomes, mitochondria, etc.).

*The sum of the starred components should be 100%.

6. TOTAL STORAGE = sum of 2a, 3a, and 4.

7. TOTAL CARBON-CONTAINING CYTOPLASM = storage + cytoplasm + chloroplast (3b + 5 + 6); does not include vacuole or wall.

8. "METABOLIZING" BIOVOLUME = cellular components that are active metabolically; cytoplasm plus chloroplast (does not include vacuole, wall, or storage).

Summaries of the quantitative results are presented in Tables 4 and 5. The following points were noted for the individual species:

Anabaena flos-aquae

Inappropriate field fixation and the resultant collapse of individual gas vesicles probably has led to an underestimation of the relative volume of the "pseudovacuole" category. No attempt was made to select for cyanophycin granules or polyphosphate bodies in the micrographs; therefore the values obtained should be an unbiased estimate of the occurrence of these inclusions within the field population. The extremely low volume fractions may be indicative of the environmental conditions at the time of sampling.

Stephanodiscus binderanus and _Fragilaria capucina_

As might be expected, the volume fraction of frustule was higher in _F. capucina_ than in _S. binderanus_. Both diatoms have a large volume fraction of vacuole as well as lipid in the vacuole. Another common feature between the diatoms is the percentage of carbon-containing cytoplasm, which is slightly larger than 50%.

Euglena viridis

The most noticeable feature encountered in _Euglena_ was the high percentage of storage products (paramylon). The reservoir (vacuole) and the contractile vacuole accounted for a higher volume fraction than was expected (16%). The pellicular ridges also occupied approximately the same volume fraction as the frustule in _Stephanodiscus_ and the cell wall in _Anabaena_.

TABLE 4. PERCENT VOLUMES OF CYTOPLASMIC COMPARTMENTS IN EIGHT PHYTOPLANKTON SPECIES
VALUES REPORTED ARE THE MEAN ± 1 S.E.

	A. flos-aquae	S. binderanus	F. capucina	E. viridis	C. erosa	P. lindemanni	Hap. 1	Hap. 2
1. Cell Wall	5.5 ± 0.27	6.8 ± 1.25	20.3 ± 0.69	5.9 ± 0.90	-0-	11.5 ± 1.23	13.3 ± 0.55	-0-
2. Total Vacuole	28.5 ± 1.12	61.6 ± 2.89	35.9 ± 1.91	15.8 ± 1.53	8.0 ± 0.94	10.2 ± 0.84	21.2 ± 1.46	2.2 ± 0.23
A. Vac. Storage	-0-	20.3 ± 2.30	12.9 ± 2.01	-0-	-0-	-0-	-0-	-0-
B. "Empty" Vac.	28.5 ± 1.12	41.3 ± 3.25	23.0 ± 1.62	15.8 ± 1.53	8.0 ± 0.94	10.2 ± 0.84	21.2 ± 1.46	2.2 ± 0.23
3. Total Chloroplast	-0-	14.3 ± 1.36	18.9 ± 1.53	22.3 ± 1.61	46.5 ± 1.82	18.9 ± 0.85	26.7 ± 1.36	36.3 ± 1.10
A. Chlor. Storage		1.6 ± 0.26	0.4 ± 0.11	-0-	24.3 ± 1.56	-0-	3.6 ± 0.75	8.3 ± 0.73
B. Chl.-Chl. Stor.	1.4 ± 0.28 (N)	12.6 ± 1.27	18.5 ± 1.51	-0-	22.2 ± 1.19	18.9 ± 0.85	23.1 ± 1.18	28.0 ± 0.86
4. Cytoplasmic Stor.	0.5 ± 0.13 (F)	-0-	-0-	33.6 ± 2.44	-0-	19.7 ± 1.53	3.6 ± 0.37	7.6 ± 0.65
5. Cytoplasm	64.1 ± 1.16	17.2 ± 2.04	24.9 ± 1.27	22.4 ± 1.27	45.5 ± 1.55	39.7 ± 1.57	35.2 ± 1.41	53.8 ± 1.18
6. Total Storage (Carbon)	-0-	22.0 ± 2.32	13.3 ± 2.00	33.6 ± 2.44	24.3 ± 1.56	19.7 ± 1.53	7.1 ± 0.75	15.9 ± 0.94
7. Carbon-Containing Cytoplasm	65.5 ± 1.21	51.8 ± 3.15	56.8 ± 1.86	78.3 ± 1.90	92.0 ± 0.94	78.3 ± 1.56	65.5 ± 1.55	97.8 ± 0.23
8. "Metabolizing" Biovolume	64.1 ± 1.16	29.9 ± 2.41	43.5 ± 1.98	44.6 ± 1.93	67.7 ± 1.59	58.6 ± 1.62	58.3 ± 1.60	81.9 ± 0.91

TABLE 5. ABSOLUTE VOLUMES OF DEFINED AREAS IN THE ALGAE
NUMBERS WERE CALCULATED USING THE MORPHOMETRICALLY-DERIVED PERCENTAGES
FOUND IN TABLE 4 FOR THESE COMPONENTS, AND THE ABSOLUTE VOLUMES
OF THE ORGANISMS CALCULATED BY ASSUMING A REGULAR GEOMETRIC FIGURE (TABLE 2)

	A. flos-aquae	S. binderanus	F. capucina	E. viridis	C. erosa	P. lindemanni	Hap 1	Hap 2
Total Carbon-containing Cytoplasm	52	430	230	2400	1200	8600	66	68
Metabolizing Biovolume	51	250	170	1400	880	6400	58	57
Naked Colorplast	--	100	74	690	290	2100	23	20

Cryptomonas erosa

The three major divisions of cellular compartments accounting for 92% of the volume of Cryptomonas were cytoplasm, chloroplast, and storage products. The remaining 8% of the volume was the anterior furrow and gullet. Consequently, Cryptomonas had one of the highest carbon-containing cytoplasm values.

Peridinium lindemanni

P. lindemanni had a total storage volume percent that was near the middle of the range across all eight species. This was not obvious from the pictures; the dinoflagellates had many small starch grains and lipid droplets.

Prymnesiophycean Algal Species 1 and 2

The differences between these species were as great as the differences between the diatoms examined. Total vacuole differed by a factor of 10; the wall volume percents were 13.3 ± 0.55 and nil; the total storage differed by a factor of 2.

DISCUSSION

The fact that environmental factors affect the cytology and morphological placticity of cells is easily documented in the literature. Studies of morphological and cytological variations are most easily accomplished by the use of synchronized cultures. The information derived from culture studies, supplemented with studies of naturally-occurring species, can be used to morphologically characterize algal species occurring in phytoplankton.

One of the most extensive reviews relating cytology to cultural conditions was made by Wilkinson and Duguid (1960) with bacteria. The authors stress the importance of synchronized cultures for morphological studies since the cytology is greatly dependent upon the life cycle stage. In addition, culture conditions, such as excess or absence of nutrients, modify the cytology, the degree of modification being dependent upon the particular life cycle. Other examples of cytological modification are abundant. Clear-cut modifications relating to environmental conditions are most easily demonstrated in both bacteria and blue-green algae. This is due inherently to the fact that they are prokaryotes, and have a relatively simple cell organization. No organelles are present and a number of storage inclusion bodies can be present depending on the immediate environment of the cell (Jensen and Sicko, 1971; 1973; 1974; Sicko, 1974; Sicko-Goad and Jensen, 1976).

Cytological and morphological variation, as a manifestation of changing environmental conditions, is also evident in organisms that possess more complex cellular organization (eukaryotes). However, as the cellular complexity increases, the number of sites that can be affected in the cells also increases. Along with the increase in complexity, there is generally an increase in cell size. Consequently the effects can be more diverse, and are located in a much larger volume.

Collyer and Fogg (1955) demonstrated that different species of algae tend to have similar relative amounts of protein, fats, and carbohydrates when grown under similar environmental conditions. Fogg (1966) stated that differences between algal classes in respect to their percent composition tend to be small when compared to the differences a single algal species may show during the course of growth in culture. This demonstrates that both the environment and the growth cycle of the cell are important in determining the biochemical composition of the cell.

The effects of changes in light intensity on algae have been studied more extensively than any other parameter. Sorokin and Krauss (1958, 1965) found that, in five green algae, increasing light intensity during growth initially favors cell division. After the optimum light intensity is reached, further increases are inhibitory to cell division.

Brown and Richardson (1968) studied the effects of different growth light intensities on various physiological processes in a variety of algae. They found that the volume of both cells and chloroplasts decreased with increasing light intensity. In most cases, the pigment content varied directly with chloroplast size. Unlike most studies of light effects, this study also demonstrates a number of other morphological changes as a result of varying growth illumination. The most notable of these effects were:

1. Cell vacuolization increased with increasing light intensity in *Amphidinium* and *Cryptomonas ovata* var. *palustris*.

2. A cell volume maximum was dependent on growth light intensity in *Chlorella*.

3. Some species such as *Euglena gracilis* exhibited a steady growth increase with increasing illumination, whereas in *Nitzschia closterium*, growth was light-dependent only at low intensities.

Morphological changes also occur as a result of cell cycle and nutrients. Messer and Ben-Shaul (1972) demonstrated that, in *Peridinium*, cell size and chlorophyll content increased during early growth and decreased with culture age. Aged chloroplasts were narrower, had fewer thylakoids, and also had a greater association with endoplasmic reticulum and cytoplasmic ribosomes. They also found that the large number of chloroplasts per cell correlated with a high chlorophyll content. Holmes (1966) demonstrated that, in four marine diatoms, nitrate, silicate, and phosphate deficiency resulted in both a reduction in chlorophyll *a* and a concomitant decrease in the number of chromatophores. The nutrient deficiencies caused a cessation of chlorophyll synthesis whereas the reduction in chromatophore number was a result of division failure rather than degeneration.

Atkinson et al. (1974) first utilized electron microscopic morphometric methods to determine the volume fraction of certain cellular compartments in

Chlorella. They demonstrated that cellular organelles were able to grow continuously throughout the cell cycle. Consequently, the average volume percents were 40% for chloroplast, 3% for the mitochondrion, and 10% for vacuoles and nucleus throughout the cycle. The components that were of particular interest were the vacuole, starch, and pyrenoid. Because *Chlorella* contains no large central vacuole, it had previously been assumed that the area of the tonoplast was insignificant. The authors confirmed that the tonoplast has an area equal to at least a third of the plasmalemma area. This indicates that the small vacuoles randomly scattered throughout the cytoplasm do contribute significantly to both the total cell volume as well as to the tonoplast area, which is also believed to contribute to solute absorption in plant cells (Laties, 1969; Humphreys, 1973).

Atkinson et al. (1974) also correlated starch reserves to respiratory activity of the cell. Starch appeared to function as a reserve material that sustained cytokinesis in the absence of photosynthesis. The onset of photosynthesis resulted in a recovery of starch reserves that were depleted during cytokinesis in the dark phase of cell synchronization. Consequently, starch reserves were quite dependent on both the photosynthetic and respiratory activities of the cell.

Both the qualitative and quantitative results presented in these few examples indicate that morphological characterization of all algal species is highly dependent upon a wide variety of parameters. Although these parameters can be easily regulated in a culture situation, the effects produced in culture studies are not easily applied to natural assemblages where a wide variety of parameters may be changing simultaneously. Biovolume estimates are used to assess the importance of algal species since phytoplankton standing crop is often converted into biomass through cell volume determinations (Nalewajko, 1966). Cell volume data are also used to extrapolate to organic carbon content, ash-free dry weight, and chlorophyll (Paasche, 1960; Mullin et al., 1966; Strathmann, 1967).

We feel that our results indicate that the inherent cellular organization of some species contributes significantly to the error of such biomass calculations. This problem was first recognized by Lohmann (1908) who indicated that only a small proportion of a large diatom is occupied by chloroplasts and cytoplasm, with the remainder of the cell being vacuole. Lohmann (1908) suggested that this should be taken into account when comparing the productive capacity of cells and their cell volumes, since the cytoplasm may form only a layer of 2 m around the cell periphery. Paasche (1960) and Strathmann (1967) have both used such correction factors and found that cell carbon, in many instances, correlates better with surface area than cell volume for diatoms. These techniques have also been utilized recently by Bellinger (1974).

The morphometric methods utilized in the present study demonstrate that both cell vacuole and cell wall play an important role as "inert" structures in all the algal species examined, not only the diatoms. In Table 5, we have calculated the corrected cellular volumes of carbon-containing structures in the cell, metabolizing biovolume (that portion of the cell other than inert structures such as cell wall and vacuole, and storage products), and chloroplast volume. When one does not include cell wall or vacuole in the volume estimates, the carbon-containing cytoplasm percentage drops significantly. Consequently, correction factors are not only applicable to large diatoms. Small vacuoles scattered throughout the cytoplasm may significantly alter biomass and cell carbon estimates.

One of the most important features of the morphometric study is that the eight algal species were all taken from water masses with similar chemical and physical properties. Consequently, the number of environmental parameters that have been demonstrated in the literature to affect the cytology of a variety of organisms is reduced. Although we are not sure that all algal species were growing under optimal conditions, it is likely that the results presented here more closely resemble the percentages that would be found in a naturally-occurring assemblage during the spring quarter than would cultured algal species. In this respect, the corrected biovolume estimates as presented are better than those derived by use of geometrical formulae alone.

The most obvious example of corrected biovolume estimates from our data is the case of the two diatoms, *S. binderanus* and *F. capucina*. The quantitative results show that, in both species of diatom, over 40% of the cell is occupied by frustule and vacuole. These two taxa also exhibit large significant differences in both frustule and vacuole relative volumes, even though they belong to the same "physiological" group. Such data suggest that cell volumes derived from geometrical formulae may differ significantly from the real quantity being sought, such as mg cellular carbon or metabolizing biomass, and the correction factor is probably not a constant for a given class of algae. Since, of all the groups examined in this study, wall and vacuole categories attain their largest cellular fractions in diatoms, errors in cell volume calculations based on shape will be particularly large in systems such as the Great Lakes where diatoms comprise a significant part of the assemblage.

Only a small fraction of the total storage in both diatom species is associated with the chloroplast. The remaining storage products, 13-20% of total cellular volume, were localized within the vacuole; approximately half of the vacuolar area in both taxa was occupied by storage. Since storage products are known to accumulate in senescent cells, percent storage may be a useful indicator of cell growth conditions.

We feel that this study of cell volume components is important for several reasons:

1. The chemical composition across algal phyla varies. This is especially significant in species that possess non-metabolizable mineralized scales or walls, which make up a considerable percentage of the total cell volume.

2. The cytological characteristics of the numerous algal species also vary. Consequently, the percentage of various components, such as vacuole, is not consistent either between phyla or between similar species.

3. Cytological compartments or volumes are subject to change with changing environmental parameters. Certain features, such as the presence of large amounts of storage products, are indicative of senescent cells. The use of morphometric methods allows one to detect morphological changes that might otherwise go undetected. One does not have to rely solely on gross morphological changes to detect significant differences between cells.

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SECTION 3

LUXURY CONSUMPTION, STORAGE, AND TRANSPORT OF PHOSPHORUS IN SAGINAW BAY

INTRODUCTION

Polyphosphates are linear condensed phosphates with an elementary formula of $M_{n+2}P_nO_{3n+1}$. They may range in size from a chain length of 2 (Pyrophosphate) to Kurrol's and Maddrell's salts of chain length of around 10^4 (Harold, 1966). Polyphosphates are stable in alkali, but acid-labile.

Lower plants (Keck and Stich, 1957), bacteria (Harold, 1966), blue-green algae (Sicko, 1974), and a variety of other organisms are known to accumulate and store large quantities of polyphosphate when grown under conditions of unlimited available phosphorus. This phenomenon is amplified when the organisms are grown under conditions of phosphate limitation and then placed under conditions of available phosphate (Mackereth, 1953; Liss and Langen, 1962; Shapiro, 1967; Sicko-Goad and Jensen, 1976). This type of storage has been termed "luxury storage" (Shapiro, 1968) and has also been referred to as the polyphosphate "overplus" phenomenon (Voelz et al., 1966).

The physiological roles of phosphagen (Kornberg, 1957; Winder and Denneny, 1955; Suzuki et al., 1972) and phosphorus reserve (Voelz et al., 1966; Harold, 1966; Kaltwasser, 1962) have been ascribed to polyphosphate. The occurrence of polyphosphate has most often been related to several physiological conditions:

1. Nutrient imbalance other than phosphate,
2. Restoration of phosphorus supply following phosphorus starvation, and
3. Nucleic acid imbalance.

The ecological significance of polyphosphate in algal cells is not well understood. Although its presence has most often been related to nutrient imbalance, the presence of polyphosphate as a phosphorus storage form in naturally-occurring species has not been well documented.

During a study of phytoplankton populations from Saginaw Bay, algal cells were routinely examined by a variety of microscopic techniques for the presence of polyphosphate bodies. The results of the survey are presented in this report.

MATERIALS AND METHODS

Most samples were collected and fixed during the routine cruises according to the schedule outlined in the previous section. Exception to this schedule was made in several cases where shoreline samples were obtained in addition to the routine sampling periods. In these cases, plankton tows were also fixed by placing the algae in veronal acetate buffer at pH 6.2 for 3 hours at room temperature (Pankratz and Bowen, 1963). The algae were then dehydrated and embedded in the routine manner.

LIGHT MICROSCOPY

Algal suspensions were stained for polyphosphates by the method of Ebel et al. (1958) and Jensen (1968). This staining procedure employs the ability of lead salts to complex with polyphosphate and remain stable at low pH values. The algae were initially fixed in 3% glutaraldehyde in 0.1M cacodylate buffer adjusted to pH 7.2 for a period of 1 hour at 4°C. The algae were then rinsed five times in 0.1M cacodylate buffer, and incubated in 20% lead nitrate, adjusted to pH 3.4 with acetic acid, for 4 hours at room temperature. After the incubation in lead nitrate, the algae were washed thoroughly five times with distilled water, then placed in 1% ammonium sulfide at room temperature for 1/2 hour. They were again washed with distilled water and then examined with a light microscope.

X-RAY ENERGY DISPERSIVE ANALYSIS

Sections for x-ray analysis were cut with an LKB Ultrotome III using glass knives. Section thickness was approximated either by use of interference colors or by the use of the fixed-increment planetary-gear advance mechanism of the ultramicrotome. The sections most commonly used were 0.25-0.50 μm in thickness. In several cases, thin sections (50-100 nm) were also utilized for x-ray analysis. In these cases, sections were cut with a diamond knife. All sections were mounted on 200- or 300-mesh copper grids and were examined unstained in either a JEOL JSM-U3 or JEM 100C electron microscope equipped with a Kevex Si(Li) drifted retractable detector. The geometry of the sections in relationship to the detector was at a 38.5° take-off angle. However, the grids were mounted on a hollow spectroscopic grade carbon stub at a 45° angle in order to maximize the x-ray signal. The sections were examined and analyzed at 25kV with constant working conditions of 10 mm working distance, 0.3nA specimen current, and a 100 sec live-time count at a rate of 250-300 cps.

PHOSPHATE UPTAKE IN *DIATOMA ELONGATUM*

A unialgal culture of *Diatoma tenue* var. *elongatum*, isolated from Lake Michigan in Chu-14, (Chu, 1942), was provided by Dr. C. K. Lin. Cells from 4-day-old cultures were washed three times in low phosphate Chu-14 (made without phosphate salts, but containing 0.5% soil extract). The cells were then resuspended in the low phosphate Chu-14 and incubated in a growth chamber at 20°C with a 16-hour light, 8-hour dark cycle for 68 hours. At the end of this limited phosphate period, during the 4th hour of the light cycle, the cells were packed by gentle centrifugation and suspended in medium containing 7.49 mgP/l. At the end of a 3-hour incubation under the original light and temperature conditions, the cells were harvested by centrifugation and fixed for electron microscopy as previously described. The supernatant culture medium was also analyzed for total phosphorus content.

RESULTS

A survey of both light and electron microscope preparations revealed that polyphosphate bodies were located in a variety of organisms in all segments of Saginaw Bay except segment IV. The dates and locations of the organisms containing polyphosphate bodies are found in Table 1. No samples were obtained during the first quarter.

In general, the light microscopic techniques involving lead sulfide precipitation were difficult to utilize for these samples on a routine basis. Polyphosphate bodies, when they were present, were very small and difficult to resolve with the light microscope. This was especially apparent in the granular blue-green algae. Examination with the electron microscope of the samples suspected to contain these inclusions proved that the assumption about their small size was correct.

The electron micrographs (Figs. 1-4) demonstrate that the polyphosphate bodies encountered were morphologically similar to the inclusions described by other authors. Most notably, the inclusions are electron dense and exhibit sublimation pockets when exposed to the electron beam for a short period of time. The polyphosphate bodies were found in a variety of organisms, but most often in bacteria, green and blue-green algae, and in diatoms. The inclusions were of special interest in the diatoms because they were most commonly found in the large central vacuoles and were sometimes found in association with polysome-like inclusions.

Since the morphological characteristics of polyphosphate bodies are not well known for algal species other than blue-green algae, experiments were undertaken to induce their formation and study their morphological variability. Cells of *Diatoma tenue* var. *elongatum* from an exponential culture were transferred to a phosphate-limiting culture medium for a period of approximately 3 days to induce several cell divisions and subsequent phosphate limitation. The cells were then transferred to Chu-14 medium containing normal phosphate levels. After 3 hours of incubation in this medium, the cells contained what appeared to be numerous small polyphosphate bodies, located in the central vacuole. The inclusions were often found associated with the polysome-like inclusions present in the vacuole. X-ray energy dispersive analysis of the vacuolar region demonstrated that this region contained quantities of both phosphorus and silicon in addition to lower levels of other background elements. During the 3-hour incubation period, the phosphorus content of the medium dropped to 6.61 mgP/l. Since

TABLE 1. DISTRIBUTION OF POLYPHOSPHATE BODIES IN NATURALLY-OCCURRING PHYTOPLANKTON IN SAGINAW BAY

Date Collected	Station	Depth	Segment
5/3/75	12	1 m	I
5/3/75	52	1 m	V
6/9/75	18	surface bloom (Anabaena)	II
6/27/75	56	1 m	III
6/27/75	12	1 m	I
5/14/76	26	1 m	III
6/17/76	26	1 m	III
7/16/75	12	1 m	I
7/16/75	18	1 m	II
7/31/75	26	1 m	III
7/31/75	52	1 m	V
8/19/75	52	1 M	V
7/8/76	Caseville	surface tow	V
7/7/76	7	1 m	I
8/5/76	Port Austin	surface tow	V
9/1/76	26	1 m	III
8/30/76	35	1 m	II
10/5/76	7	1 m	I
10/5/76	22	1 m	II
10/8/76	26	1 m	III
10/7/76	51	1 m	V
10/7/76	52	1 m	V
10/8/76	56	1 m	III

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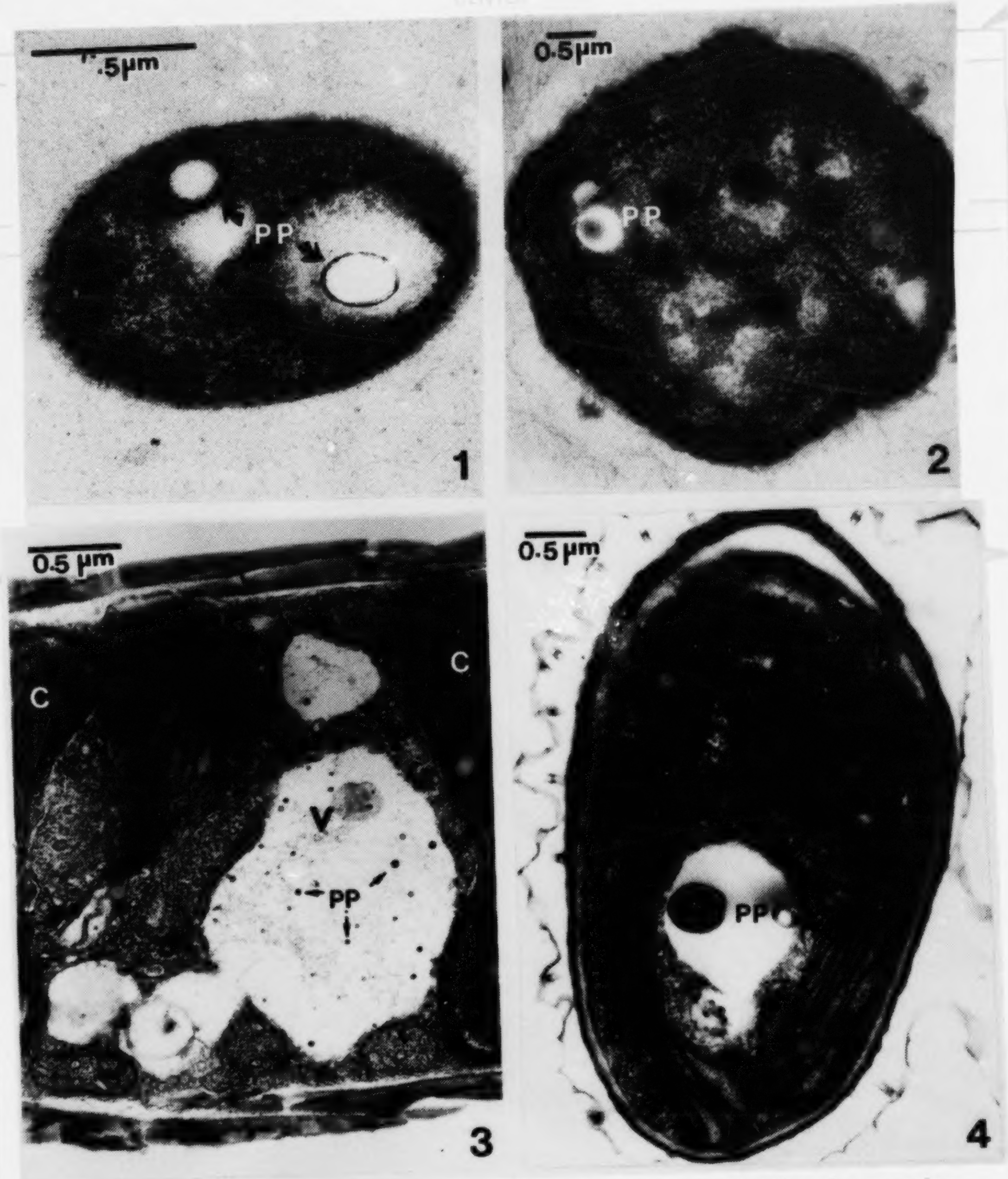

Figures 1-4. Electron micrographs of polyphosphate bodies in species of phytoplankton from Saginaw Bay. Magnifications are indicated by bar in upper left of each figure. Figure 1. An undetermined small blue-green alga with large polyphosphate (PP) bodies in both electron lucent and electron dense regions of the cell. Figure 2. Anacystis sp. with polyphosphate bodies (PP). Figure 3. Fragilaria capucina with small polyphosphate bodies (pp) in the vacuole (V), which is surrounded by the chloroplasts (C) and other cellular organelles. Figure 4. Scenedesmus sp. with large polyphosphate bodies in the vacuole.

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the morphological characteristics were similar to the polyphosphate bodies found in the diatoms collected from natural assemblages, the naturally-occurring polyphosphate bodies were analyzed in a similar fashion. The results of these analyses are presented in Figures 5-7.

DISCUSSION

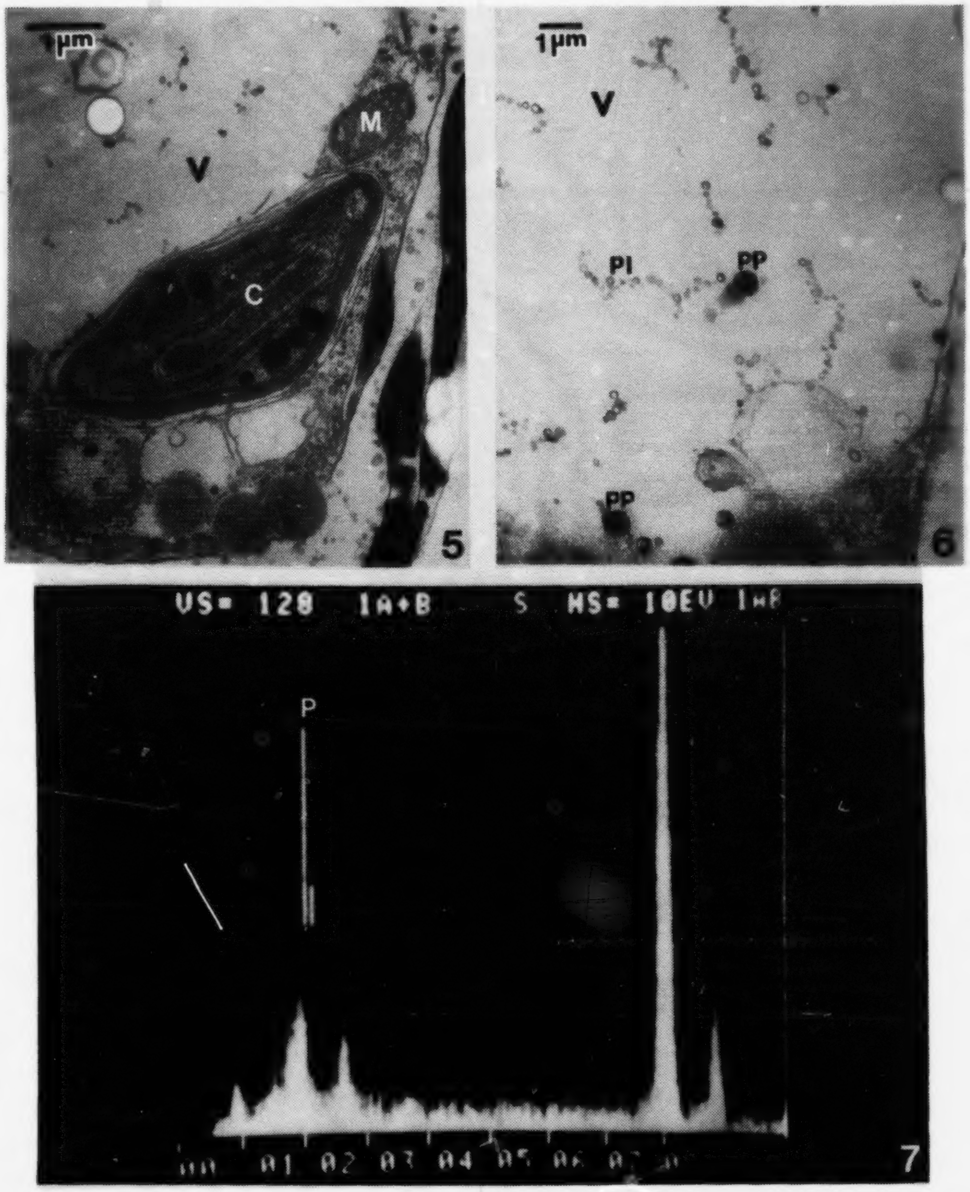
Although the sampling was limited, we found that polyphosphate bodies were present in a variety of organisms in Saginaw Bay in all segments except segment IV. The use of lead sulfide precipitation to detect their presence can be somewhat misleading because the polyphosphate bodies found in these organisms were quite small and difficult to resolve with the light microscope. The use of the electron microscope and related techniques were necessary to confirm their presence.

Additional shoreline samples were obtained during July and August, 1976. This was necessitated by the fact that the routine method of fixation employing glutaraldehyde in the field changed the morphology of the polyphosphate bodies, especially in the prokaryotes. Since this was expected (Jensen et al., 1977), and since a number of extracted polyphosphate bodies were encountered, especially in *Anabaena*, shoreline tows were made and the cells were also fixed in modified osmium, using no glutaraldehyde. This method of fixation proved to be superior for the prokaryotes.

When inclusions were encountered that were suspected to be polyphosphate bodies, x-ray energy dispersive analysis was used to confirm the presence of phosphorus. This technique was useful when either there was a large number of bodies located in one central area or the polyphosphate bodies were large. A few small bodies generally did not provide enough x-ray emission above background to prove conclusively that phosphorus was present. Consequently, Table 1 includes only those stations where the presence of polyphosphate was confirmed and not merely suspected.

The most interesting results of the study were obtained both with *Fragilaria capucina*, collected from a natural assemblage, and *Diatoma tenue* var. *elongatum*, a cultured species. *F. capucina* had numerous small polyphosphate bodies located in its vacuole, and often in association with polysome-like inclusions. The x-ray spectrum of the vacuolar region demonstrated that phosphorus, osmium, and silicon were present in this region. Although the osmium can be accounted for, as a result of the fixative, the silicon remains somewhat puzzling. Since the morphology of the polyphosphate bodies was not what was expected and since it has not been adequately described in diatoms, attempts were made to induce polyphosphate body formation in a cultured diatom through phosphate imbalance. The results of the experiment demonstrated the polyphosphate bodies encountered were quite similar to those found in the naturally-occurring species. The size range, location, and x-ray spectrum were all similar. In addition, the association with polysome-like inclusions was even more frequent. This is not surprising in view of the literature.

TYPING GUIDE SHEET



Figures 5-7. Polyphosphate bodies in Diatoma tenue var. elongatum. Magnifications of electron micrographs indicated by scale bar in upper left of figures. Figure 5. Marginal region of the cell showing chloroplast (C), mitochondria (M), and the vacuole (V). Electron dense structures in the right of the figure are elements of the siliceous wall. Figure 6. Vacuolar (V) region of cell. Polyphosphate (PP) bodies appear to be formed in linear arrays of polysome-like (Pl) bodies. Figure 7. X-ray spectrum of polyphosphate bodies shown in Figure 6. Phosphorus peak (P) is indicated.

Jensen (1969) demonstrated that, in Plectonema boryanum, polyphosphate bodies frequently developed in the ribosomal areas of the cytoplasm. Sicko (1974) found that, under conditions of phosphate imbalance, polyphosphate bodies developed in association with strands of DNA in the nuclear area of P. boryanum. It was postulated that the DNA strands, along with short chained polyphosphates, could serve as primers for the polymerization of the longer chained acid-insoluble polyphosphates.

The relationship between nucleic acids and polyphosphate is further complicated by studies which indicate that ribonucleic acid and polyphosphate may exist as a complex in several organisms. This complex was first postulated by MacFarlane (1936). RNA-polyphosphate has been demonstrated by Kulaev and Belozerskii (1958) in Aspergillus niger, by Chayen et al. (1955) in Torulopsis utilis, by Winder and Denneny (1957) in Mycobacteria, by Ebel et al. (1958, 1962) in yeast, by Correll and Tolbert (1962, 1964) and by Correll (1965) in Anabaena and Chlorella. Correll and Tolbert (1962, 1964) found that, in Anabaena, the complex accounted for 25-35% of the total phosphorus, and a major portion of the alga's RNA. However, there was an additional 40-50% of the total phosphorus present as uncomplexed polyphosphate. The polyphosphate-RNA complex in Chlorella was more variable; the relative amounts of the complex varied with respect to the synchronized growth cycle.

The ecological causes and consequences of polyphosphate storage in phytoplankton may be important in evaluating the impact areas, such as Saginaw Bay, on the rest of the Great Lakes system. Although this preliminary study does not provide sufficient basis to fully determine the importance of the process, a number of points are evident.

On the basis of the literature and the number of experiments carried out with phytoplankton species native to the Great Lakes, it is evident that the accumulation of phosphorus in the form of polyphosphate bodies may be triggered by any one of a number of mechanisms which interfere with normal cellular growth processes. In a sense, the process provides a mechanism whereby organisms may protect their ability to sequester the crucial limiting nutrient phosphorus even in the presence of other growth limitations. The most commonly observed condition inducing polyphosphate body formation is phosphorus limitation followed by resupply of the nutrient at concentrations above the immediate growth needs or capabilities of the cells. The process may also be induced by conditions where adequate phosphorus supplies are present, but growth is limited by concentration of some other nutrient or factor. Polyphosphate body formation may also apparently be initiated by low level toxic stress on the cells, sufficient to restrict maximum growth rates.

The observed distribution of phytoplankton populations containing polyphosphate bodies is consistent with any one, or a combination of, these mechanisms. On the basis of our limited observations, populations containing polyphosphate bodies are frequent in segments 1, 3, and 5, rare in segment 2, and not present in segment 4. These results imply that exposure to factors inducing polyphosphate body formation is probably greatest in segment 1, and affected populations are then entrained in the normal circulation pattern of the bay. It is particularly interesting that the abundance of polyphosphate bodies corresponds to the usual pattern of greatest total phytoplankton density and to the most probable area of excursion of materials from the bay. Within this area the relative abundance of cells containing polyphosphate bodies appears to be quite uniform.

The most probable consequence of polyphosphate body formation is a temporal separation of phosphorus uptake from eventual resultant growth. In some cases cells which have sequestered phosphorus in excess of their immediate needs may perish before utilizing the reserve. The population, as a whole, however could be expected to exhibit a delayed growth response. This phenomenon may account, in part at least, for the persistent pattern of high phytoplankton abundance at stations along the southern coast of Saginaw Bay. In a system like Saginaw Bay which has dynamic circulation patterns, the delayed response also implies responses in areas some distance removed from the primary source of phosphorus enrichment. This is probably the most important aspect of the problem in the general case of the Great Lakes. Potentially obnoxious populations developed in areas of high nutrient loading could exit the immediate area of effect carrying with them the potential for growth, even under phosphorus-limited conditions. The largest potential expression of the effect would be expected to occur in the blue-green algae, which are apparently subjected to minimal sinking and predation losses. We regard this mechanism as a probable explanation for the extreme dispersal of certain blue-green algal populations from Saginaw Bay into Lake Huron observed by Schelske et al. (1974) and Stoermer and Kreis (1980).

We had previously assumed that polyphosphate body formation was important only in prokaryotic organisms. The results of this study suggest that the mechanism is present in most of the major physiological groups present in the Great Lakes. Notable exeptions seem to be the Cryptomonads and Dinoflagellates. Although we have not attempted induction in species of these groups under experimental conditions, none of the wild populations examined contained polyphosphate bodies. Representatives of all of the other major algal physiological groups did. Most of the species examined in the study are usually associated with eutrophied conditions in the Great Lakes and it is possible that luxury consumption of phosphorus is one of the factors which confers competitive advantage on these populations. Further research will be needed to answer this question.

Our results also indicate that heavy metals may also be sequestered in polyphosphate bodies. This mechanism is physiologically plausible and may be important in biological transport of toxic materials. We are investigating this problem at the present time.

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APPENDIX 1. PHYTOPLANKTON OF SAGINAW BAY (LAKE HURON), 1974-1976

BACILLARIOPHYTA

Achnanthes affinis Grun.
Achnanthes biasolettiana (Kütz.) Grun.
Achnanthes bioreti Germain
Achnanthes clevei Grun.
Achnanthes clevei var. *rostrata* Hust.
Achnanthes exigua Grun.
Achnanthes exigua var. *heterovalva* Krasske
Achnanthes flexella (Kütz.) Brun
Achnanthes flexella var. *alpestris* Brun
Achnanthes hungarica (Grun.) Grun.
Achnanthes lanceolata (Bréb.) Grun.
Achnanthes lanceolata var. *dubia* Grun.
Achnanthes lanceolata var. *omissa* Reim.
Achnanthes lapponica (Hust.) Hust.
Achnanthes lapponica var. *ninckei* (Guerm. and Mang.) Reim.
Achnanthes linearis (W. Sm.) Grun.
Achnanthes microcephala (Kütz.) Grun.
Achnanthes minutissima Kütz.
Achnanthes minutissima var. *cryptocephala* Grun.
Achnanthes oestrupii var. *lanceolata* Hust.
Actinocyclus normanii fo. *subsalsa* (Juhl.- Dannf.) Hust.
Amphipleura pellucida (Kütz.) Kütz.
Amphora cruciferoides Stoerm. and Yang
Amphora ovalis (Kütz.) Kütz.
Amphora ovalis var. *affinis* (Kütz.) V.H.
Amphora ovalis var. *pediculus* (Kütz.) V.H.
Amphora perpusilla (Grun.) Grun.
Amphora subcostulata Stoerm. and Yang
Amphora veneta var. *capitata* Haworth
Anomoeoneis vitrea (Grun.) Ross
Asterionella formosa Hass.
Caloneis alpestris (Grun.) Cl.
Caloneis bacillum (Grun.) Cl.
Caloneis bacillum var. *lancettula* (Schulz) Hust.
Caloneis sp. #3
Caloneis ventricosa var. #1
Cocconeis diminuta Pant.
Cocconeis fluviatilis Wallace
Cocconeis pediculus Ehr.
Cocconeis placentula Ehr.
Cocconeis placentula var. *euglypta* (Ehr.) Grun.
Cocconeis placentula var. *lineata* (Ehr.) V.H.
Cocconeis sp.#2
Cocconeis thumensis A. Mayer

(continued).

APPENDIX 1. (continued).

Cyclotella antiqua W. Sm.
Cyclotella atomus Hust.
Cyclotella comensis Grun.
Cyclotella comta (Ehr.) Kütz.
Cyclotella cryptica Reimann, Lewin and Guillard
Cyclotella kuetzingiana Thw.
Cyclotella kuetzingiana auxospore
Cyclotella meneghiniana Kütz.
Cyclotella meneghiniana var. *plana* Fricke
Cyclotella michiganiana Skv.
Cyclotella ocellata Pant.
Cyclotella operculata (Ag.) Kütz.
Cyclotella sp. auxospore
Cyclotella stelligera (Cl. and Grun.) V.H.
Cyclotella stelligera auxospore
Cyclotella temperei M. Perag. and Hérib.
Cymatopleura elliptica (Bréb. and Godey) W. Sm.
Cymatopleura solea (Bréb. and Godey) W. Sm.
Cymatopleura solea var. *apiculata* (W. Sm.) Ralfs
Cymbella affinis Kütz.
Cymbella amphicephala Näg.
Cymbella cesatii (Rabh.) Grun.
Cymbella cistula (Ehr.) Kirchn.
Cymbella cuspidata Kütz.
Cymbella delicatula Kütz.
Cymbella hybrida Grun.
Cymbella leptoceros var. *rostrata* Hust.
Cymbella microcephala Grun.
Cymbella microcephala var. *crassa* Reim.
Cymbella minuta Hilse
Cymbella minuta var. *silesiaca* (Bleisch) Reim.
Cymbella minuta fo. *latens* (Krasske) Reim.
Cymbella muelleri fo. *ventricosa* (Temp. and Perag.) Reim.
Cymbella obtusiuscula Kütz.
Cymbella parvula Krasske
Cymbella prostrata (Berk.) Cl.
Cymbella prostrata var. *auerswaldii* (Rabh.) Reim.
Cymbella sinuata Greg.
Cymbella sp. #1
Cymbella sp. #6
Cymbella sp. #10
Cymbella subventricosa Choln.
Cymbella triangulum (Ehr.) Cl.
Cymbella tumida (Bréb.) V.H.
Cymbella turgida var. *pseudogracilis* Choln.
Cymbella ventricosa Ag.

(continued).

APPENDIX 1. (continued).

Denticula tenuis var. *crassula* (Näg.) W. and G.S. West
Diatoma tenue Ag.
Diatoma tenue var. *elongatum* Lyngb.
Diatoma tenue var. *pachycephala* Grun.
Diatoma vulgare Bory
Diploneis boldtiana Cl.
Diploneis oculata (Bréb.) Cl.
Diploneis parma Cl.
Entomoneis ornata (J.W. Bail.) Reim.
Epithemia intermedia Fricke
Epithemia sorex Kütz.
Epithemia turgida (Ehr.) Kütz.
Fragilaria brevistriata Grun.
Fragilaria brevistriata var. *inflata* (Pant.) Hust.
Fragilaria capucina Desm.
Fragilaria capucina var. *lanceolata* Grun.
Fragilaria capucina var. *mesolepta* Rabh.
Fragilaria construens (Ehr.) Grun.
Fragilaria construens var. *binodis* (Ehr.) Grun.
Fragilaria construens var. *minuta* Temp. and M. Perag.
Fragilaria construens var. *pumila* Grun.
Fragilaria construens var. *venter* (Ehr.) Grun.
Fragilaria crotonensis Kitton
Fragilaria crotonensis var. *oregona* Sov.
Fragilaria intermedia Grun.
Fragilaria intermedia var. *fallax* (Grun.) A. Cl.
Fragilaria leptostauron (Ehr.) Hust.
Fragilaria leptostauron var. *dubia* (Grun.) Hust.
Fragilaria pantocsekii var. *binodis* (Pant.) A. Cl.
Fragilaria pinnata Ehr.
Fragilaria pinnata var. *intercedens* (Grun.) Hust.
Fragilaria pinnata var. *lancettula* (Schum.) Hust.
Fragilaria vaucheriae (Kütz.) Peters.
Frustulia vulgaris (Thw.) DeT.
Gomphonema acuminatum Ehr.
Gomphonema angustatum (Kütz.) Rabh.
Gomphonema angustatum var. *producta* Grun.
Gomphonema intricatum Kütz.
Gomphonema intricatum var. *pumila* Grun.
Gomphonema olivaceum (Lyngb.) Kütz.
Gomphonema parvulum (Kütz.) Kütz.
Gomphonema parvulum var. *lagenula* (Kütz.) Freng.
Gomphonema subclavata var. *mustela* (Ehr.) Cl.
Gomphonema sp. #3
Gomphonema truncatum Ehr.
Gyrosigma acuminatum (Kütz.) Rabh.

(continued).

APPENDIX 1. (continued).

Gyrosigma attenuatum (Kütz.) Rabh.
Gyrosigma scalproides (Rabh.) Cl.
Gyrosigma spencerii (Sulliv. and Wormley) Cl.
Gyrosigma spencerii var. *curvula* (Grun.) Reim.
Hantzschia amphioxys (Ehr.) Grun.
Mastogloia smithii Thw.
Melosira distans var. *alpigena* Grun.
Melosira granulata (Ehr.) Ralfs
Melosira granulata var. *angustissima* O. Müll.
Melosira islandica O. Müll.
Melosira italica subsp. *subarctica* O. Müll.
Melosira varians Ag.
Meridion circulare (Grev.) Ag.
Meridion circulare var. *constrictum* (Ralfs) V.H.
Navicula acceptata Hust.
Navicula anglica var. *subsalsa* (Grun.) Cl.
Navicula aurora Sov.
Navicula bacillum Ehr.
Navicula capitata Ehr.
Navicula capitata var. *hungarica* (Grun.) Ross
Navicula capitata var. *luneburgensis* (Grun.) Patr.
Navicula capitata var. #1
Navicula clementis Grun.
Navicula cocconeiformis Greg.
Navicula confervacea (Kütz.) Grun.
Navicula costulata Cl. and Grun.
Navicula cryptocephala Kütz.
Navicula cryptocephala var. *intermedia* V.H.
Navicula cryptocephala var. *veneta* (Kütz.) Rabh.
Navicula cuspidata (Kütz.) Kütz.
Navicula decussis Østr.
Navicula exigua var. *capitata* Patr.
Navicula explanata Hust.
Navicula gastrum (Ehr.) Kütz.
Navicula gottlandica Grun.
Navicula gregaria Donk.
Navicula heufleri var. *leptocephala* (Bréb.) Patr.
Navicula integra (W. Sm.) Ralfs
Navicula jaernefeltii Hust.
Navicula lacustris Greg.
Navicula lanceolata (Ag.) Kütz.
Navicula latens Krasske
Navicula menisculus Schum.
Navicula menisculus var. *obtusa* Hust.
Navicula menisculus var. *upsaliensis* Grun.
Navicula minima Grun.

(continued).

Navicula minuscula Grun.
Navicula mutica Kütz.
Navicula mutica var. *cohnii* (Hilse) Grun.
Navicula nyassensis fo. *minor* O. Müll.
Navicula odiosa Wallace
Navicula ordinaria Hust.
Navicula peregrina (Ehr.) Kütz.
Navicula placentula (Ehr.) Kütz.
Navicula protracta (Grun.) Cl.
Navicula protracta fo. *subcapitata* (Wisl. and Por.) Hust.
Navicula pupula Kütz.
Navicula pupula var. *rectangularis* (Greg.) Grun.
Navicula pygmaea Kütz.
Navicula radiosa Kütz.
Navicula radiosa var. *tenella* (Bréb.) Cl. and Möll.
Navicula reinhardtii Grun.
Navicula rhynchocephala Kütz.
Navicula rotunda Hust.
Navicula scutelliodes W. Sm.
Navicula sp. #7
Navicula sp. #35
Navicula sp. #43
Navicula sp. #44
Navicula sp. #55
Navicula sp. #78
Navicula spp.
Navicula stroemii Hust.
Navicula stroesii (Østr.) A. Cl.
Navicula subseminulum Hust.
Navicula terminata Hust.
Navicula tripunctata (O.F. Müll) Bory
Navicula tripunctata var. *cuneata* (Lauby) Stoerm. and Yang
Navicula tripunctata var. *schizonemoides* (V.H.) Patr.
Navicula tuscula Ehr.
Navicula tuscula fo. *obtusa* (Hust.) Hust.
Navicula vanheurckii Patr.
Navicula viridula (Kütz.) Ehr.
Navicula viridula var. *linearis* Hust.
Navicula viridula var. *rostellata* (Kütz.) Cl.
Navicula viridula var. #2
Neidium dubium (Ehr.) Cl.
Neidium dubium fo. *constrictum* (Hust.) Hust.
Neidium dubium var. #1
Nitzschia acicularioides Hust.
Nitzschia acicularis (Kütz.) W. Sm.
Nitzschia actinastroides (Lemm.) Van Goor

(continued).

APPENDIX 1. (continued).

Nitzschia acula Hantz.
Nitzschia amphibia Grun.
Nitzschia angustata var. *acuta* Grun.
Nitzschia apiculata (Greg.) Grun.
Nitzschia bacata Hust.
Nitzschia capitellata Hust.
Nitzschia commutata Grun.
Nitzschia confinis Hust.
Nitzschia denticula Grun.
Nitzschia diserta Hust.
Nitzschia dissipata (Kütz.) Grun.
Nitzschia dissipata var. *borneensis* Hust.
Nitzschia dissipata var. *media* (Hantz.) Grun.
Nitzschia filiformis (W. Sm.) Schutt
Nitzschia fonticola Grun.
Nitzschia fonticola var. *pelagica* Hust.
Nitzschia frustulum (Kütz.) Grun.
Nitzschia frustulum var. *perminuta* Grun.
Nitzschia frustulum var. *subsalina* Hust.
Nitzschia frustulum var. #1
Nitzschia gracilis Hantz.
Nitzschia holsatica Hust.
Nitzschia hungarica Grun.
Nitzschia insecta Hust.
Nitzschia interrupta (Reich.) Hust.
Nitzschia kuetzingiana Hilse
Nitzschia linearis (Ag.) W. Sm.
Nitzschia linearis var. *tenuis* (Kütz.) Grun.
Nitzschia longissima fo. *parva* Grun.
Nitzschia longissima var. *reversa* Grun.
Nitzschia palea (Kütz.) W. Sm.
Nitzschia palea var. *tenuirostris* Grun.
Nitzschia paleacea Grun.
Nitzschia recta Hantz.
Nitzschia sigma (Kütz.) W. Sm.
Nitzschia sigmoidea (Nitz.) W. Sm.
Nitzschia sp. #1
Nitzschia sp. #2
Nitzschia sp. #5
Nitzschia sp. #6
Nitzschia sp. #8
Nitzschia sp. #9
Nitzschia sp. #10
Nitzschia sp. #11
Nitzschia sp. #17
Nitzschia sp. #18

(continued).

APPENDIX 1. (continued).

Nitzschia sp. #19
Nitzschia sp. #22
Nitzschia sp. #26
Nitzschia *spiculoides* Hust.
Nitzschia *subamphioxoides* Hust.
Nitzschia *sublinearis* Hust.
Nitzschia *thermalis* (Ehr.) Auersw.
Nitzschia *thermalis* var. *minor* Hilse
Nitzschia *tryblionella* Hantz.
Nitzschia *tryblionella* var. *debilis* (Arn.) A. Mayer
Nitzschia *tryblionella* var. *levidensis* (W. Sm.) Grun.
Opephora *martyi* Hérib.
Pinnularia *brebissonii* (Kütz.) Rabh.
Pinnularia *globiceps* Greg.
Pinnularia *viridis* (Nitz.) Ehr.
Plagiotropis *lepidoptera* var. *proboscidea* (Cl.) Reim.
Rhizosolenia *eriensis* H.L. Sm.
Rhizosolenia *gracilis* H.L. Sm.
Rhoicosphlenia *curvata* (Kütz.) Grun.
Skeletonema *potamos* (Weber) Hasle
Skeletonema *subsalsum* (A. Cl.) Bethge
Stauroneis *acutiuscula* M. Perag. and Hérib.
Stauroneis *dilatata* Ehr.
Stephanodiscus *alpinus* Hust.
Stephanodiscus *astraea* (Ehr.) Grun.
Stephanodiscus *binderanus* (Kütz.) Kreig.
Stephanodiscus *hantzschii* Grun.
Stephanodiscus *minutus* Grun.
Stephanodiscus *niagarae* Ehr.
Stephanodiscus sp. auxospore
Stephanodiscus *subtilis* (Van Goor) A. Cl.
Stephanodiscus *tenuis* Hust.
Stephanodiscus *transilvanicus* Pant.
Surirella *angusta* Kütz.
Surirella *birostrata* Hust.
Surirella *biseriata* var. *diminuta* A. Cl.
Surirella *linearis* var. *constricta* (Ehr.) Grun.
Surirella *ovata* Kütz.
Surirella *ovata* var. *pinnata* (W. Sm.) Rabh.
Surirella *ovata* var. *salina* (W. Sm.) Rabh.
Surirella *ovata* var. #1
Surirella sp. #4
Synedra *acus* Kütz.
Synedra *capitata* Ehr.
Synedra *cyclopum* Brutschy
Synedra *delicatissima* W. Sm.

(continued).

APPENDIX 1. (continued).

Synedra delicatissima var. angustissima Grun.
Synedra filiformis Grun.
Synedra minuscula Grun.
Synedra montana Krasske
Synedra ostenfeldii (Kreig.) A. Cl.
Synedra parasitica (W. Sm.) Hust.
Synedra rumpens Kütz.
Synedra rumpens var. familiaris (Kütz.) Hust.
Synedra tenera W. Sm.
Synedra ulna (Nitz.) Ehr.
Synedra ulna var. chaseana Thomas
Synedra ulna var. claviceps Hust.
Synedra ulna var. danica (Kütz.) V.H.
Synedra ulna var. spathulifera (Grun.) V.H.
Tabellaria fenestrata (Lyngb.) Kütz.
Tabellaria fenestrata var. geniculata A. Cl.
Tabellaria flocculosa (Roth) Kütz.
Tabellaria flocculosa var. linearis Koppen
Thalassiosira pseudonana Hasle and Heim.
Thalassiosira weissflogii (Grun.) Fryxell and Hasle

CHRYSOPHYTA

Chrysochromulina parva Lackey
Chrysochromulina sp. #1
Chrysosphaerella longispina Lautb.
Dinobryon cylindricum Imhof
Dinobryon cylindricum cysts
Dinobryon divergens Imhof
Dinobryon sociale Ehr.
Dinobryon cysts
Hymenomonas roseola Stein
Mallomonas caudata Iwanoff
Mallomonas elongata Reverdin
Mallomonas fastigata Zach.
Mallomonas litomesa Stokes
Mallomonas producta (Zach.) Iwanoff
Mallomonas pseudocoronata Presc.
Mallomonas sp. #1
Mallomonas sp. #3
Mallomonas tonsurata var. alpina (Pasch. and Ruttn.) Kreig.
Mallomonas cysts
Ochromonas sp. #1
Spiniferomonas trioralis Takahashi
Synura uvella Ehr.
Uroglenopsis americana (Calk.) Lemm.

(continued).

APPENDIX 1. (continued).

CRYPTOPHYTA

Cryptomonas erosa Ehr.
Cryptomonas marssonni Skuja
Cryptomonas ovata Ehr.
Cryptomonas sp. #1
Cryptomonas cyst
Chroomonas nordstedtii Hansg.
Rhodomonas minuta Skuja
Rhodomonas minuta var. *nannoplanctica* Skuja
Undetermined cyst
Undetermined flagellate sp. #1
Undetermined flagellate sp. #2
Undetermined flagellate spp.

CHLOROPHYTA

Actinastrum gracilimum G.M. Sm.
Actinastrum hantzschii Lagerh.
Actinastrum hantzschii var. *fluviatile* Schroed.
Ankistrodesmus braunii (Näg.) Brunnth.
Ankistrodesmus falcatus (Corda) Ralfs
Ankistrodesmus falcatus var. *mirabilis* (West and West) G.S. West
Ankistrodesmus gelifactum (Chod.) Bourr.
Ankistrodesmus setigerus (Schroed.) G.S. West
Ankistrodesmus sp. #1
Ankistrodesmus sp. #3
Ankistrodesmus sp. #4
Binuclearia eriensis Tiffany
Borodinella polytetras Miller
Botryococcus braunii Kütz.
Cerasterias sp. #1
Characium curvatum G.M. Sm.
Chlamydomonas sp. #1
Chlorella sp. #1
Chodatella ciliata (Lagerh.) Chod.
Cladophora sp. #1
Closteriopsis sp. #1
Closterium aciculare T. West
Coccomyxa minor Skuja
Coelastrum microporum Näg.
Coelastrum proboscideum Bohlin
Coelastrum reticulatum (Dang.) Senn.

(continued).

APPENDIX 1. (continued).

Cosmarium botrytis Menegh.
Cosmarium depressum (Näg.) Lundell
Cosmarium sp. #1
Crucigenia quadrata Morren
Dictyochlorella sp. #1
Dictyosphaerium ehrenbergianum Näg.
Dictyosphaerium pulchellum Wood
Dimorphococcus sp. #1
Elaktothrix gelatinosa Wille
Eudorina elegans Ehr.
Eutetramorus sp. #1
Franceia droescheri (Lemm.) G.M. Sm.
Gloeocystis planctonica (West and West) Lemm.
Gloeocystis sp. #1
Golenkinia paucispina West and G.S. West
Golenkinia radiata (Chod.) Wille
Gonium pectorale Müll.
Kirchneriella lunaris (Kirch.) Moebius
Kirchneriella obesa var. *major* (Bernard) G.M. Sm.
Lagerheimia subsalsa Lemm.
Lobocystis sp. #1
Micractinium pusillum Fresenius
Mougeotia sp. #1
Nephrocytium agardhianum Näg.
Nephrocytium limneticum (G.M. Sm.) G.M. Sm.
Oedogonium sp. #1
Oocystis borgei Snow
Oocystis parva West and West
Oocystis solitaria Wittr.
Oocystis spp.
Palmodictyon sp. #1
Pediastrum boryanum (Turp.) Menegh.
Pediastrum duplex Meyen
Pediastrum duplex var. *clathratum* (A. Braun) Lagerh.
Pediastrum duplex var. *cohaerens* Bohl.
Pediastrum tetras (Ehr.) Ralfs.
Pedinomomas sp. #1
Phacotus lenticularis (Ehr.) Stein
Planctonema lauterbornii Schmidle
Quadrigula lacustris (Chod.) G.M. Sm.
Saturnella sp. #1
Scenedesmus abundans var. *brevicauda* G.M. Sm.
Scenedesmus acutiformis Schroed.
Scenedesmus arcuatus var. *platydisca* G.M. Sm.
Scenedesmus armatus (Chod.) G.M. Sm.
Scenedesmus bicellularis Chod.

(continued).

APPENDIX 1. (continued).

Scenedesmus bijuga (Turp.) Lagerh.
Scenedesmus bijuga var. *alternans* (Reinsch) Hansg.
Scenedesmus corallinus Chod.
Scenedesmus denticulatus var. *australis* Playfair
Scenedesmus denticulatus Lagerh.
Scenedesmus dimorphus Kütz.
Scenedesmus falcatus Chod.
Scenedesmus granulatus West and West
Scenedesmus hystrix Lagerh.
Scenedesmus incrassatulus Bohl.
Scenedesmus intermedius Chod.
Scenedesmus jovis Chod.
Scenedesmus lefervii Defl.
Scenedesmus longus Meyen
Scenedesmus quadricauda (Turp.) Bréb.
Scenedesmus quadricauda var. *longispina* (Chod.) G.M. Sm.
Scenedesmus quadricauda var. *maximus* West and West
Scenedesmus quadricauda var. *parvus* G.M. Sm.
Scenedesmus quadricauda var. *quadrispina* (Chod.) G.M. Sm.
Scenedesmus sempervirens Chod.
Scenedesmus serratus (Corda) Bohl.
Scenedesmus tetradesmiformis (Woloszynska) Chod.
Schroederia setigera (Schroed.) Lemm.
Selenastrum bibraianum Reinsch
Selenastrum westii G.M. Sm.
Selenastrum gracile Reinsch
Sestosoma sp. #1
Siderocystopsis sp. #1
Sorastrum sp. #1
Sphaerocystis schroeteri Chod.
Staurastrum paradoxum Meyen
Tetraedron caudatum (Corda) Hansg.
Tetraedron hastatum (Reinsch) Hansg.
Tetraedron minimum (A. Br.) Hansg.
Tetraedron trigonum (Näg.) Hansg.
Tetraedron trigonum var. *setigerum* (Archer) Lemm.
Tetrastrum staurogeniaeforme (Schroed.) Lemm.
Trochiscia sp. #1
Ulothrix subconstricta G.S. West
Ulothrix sp. #1
Undetermined green colony sp. #1
Undetermined green colony sp. #2
Undetermined green colony sp. #3
Undetermined green filament sp. #1
Undetermined green filament sp. #4
Undetermined green filament sp. #5

(continued).

APPENDIX 1. (continued).

Westella linearis G.M. Sm.
Xanthidium antilopaeum var. *depauperatum* West and West

CYANOPHYTA

Agmenellum quadruplicatum (Menegh.) Bréb.
Anabaena flos-aquae (Lyngb.) Bréb.
Anabaena spiroides var. *crassa* Lemm.
Anabaena subcylindrica Borge
Anabaena zinserlingii Kossinskaja
Anabaena sp. #2
Anacystis cyanea (Kütz.) Dr. and Daily
Anacystis dimidiata (Kütz.) Dr. and Daily
Anacystis incerta (Lemm.) Dr. and Daily
Anacystis thermalis (Menegh) Dr. and Daily
Aphanizomenon flos-aquae (Lyngb.) Bréb.
Chroococcus dispersus (Keissl.) Lemm.
Coccochloris sp. #1
Dactylococcopsis acicularis Lemm.
Gomphosphaeria aponina Kütz.
Gomphosphaeria lacustris Chod.
Gomphosphaeria wichurae (Hilse) Dr. and Daily
Microcoleus vaginatus (Vauch.) Gom.
Oscillatoria bornetii Zukal
Oscillatoria limnetica Lemm.
Oscillatoria retzii Ag.
Oscillatoria sp. #1
Oscillatoria sp. #2
Plectonema sp. #1
Schizothrix calcicola (Ag.) Gom.
Undetermined blue-green filament #1
Undetermined blue-green filament #2

PYRRHOPHYTA

Ceratium hirundinella (O.F. Müll.) Shrank
Glenodimium sp. #1
Gymnodinium helveticum Penard
Gymnodinium sp. #1
Hemidinium sp. #1
Peridinium aciculiferum (Lemm.) Lemm.
Peridinium cinctum (Müll.) Ehr.
Peridinium lindemanii Lef.
Peridinium sp. #1
Peridinium sp. #2

(continued).

APPENDIX 1. (continued).

EUGLENOPHYTA

Euglena allorgei Defl.
Euglena acus Ehr.
Euglena viridis Ehr.
Lepocinclis sp. #1
Phacus sp. #1
Tracholomonas lacustris Drezep.
Tracholomonas volvocina Ehr.
Trachelomonas sp. #1

SCHIZOPHYTA

Beggiatoa alba (Vauch.) Trev.